

Duration of the Prebreeding Period and Its Relation to Social Organization of the Sandpipers (Charadrii, Aves) Nesting in Northeastern Yakutia

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Abstract—The work was performed at two stations of the Ornithological Unit with the Institute of Biological Problems of the North, Far East Branch, Russian Academy of Sciences in the Nizhnekolymsk raion, Yakutia, starting from May 18–20 in 1984, 1985, 1987, 1988, and 1990. The timing of the prebreeding period has been determined for 11 sandpiper species differing in their social organization and compared using allometric equations. Body weight was chosen as the characteristic for bird size. Sandpipers arrive to the tundra at almost critical temperatures to begin breeding as early as possible. The timing of breeding depends on the foraging mode and distance to the overwintering areas. The duration of the prebreeding period is constant for each individual species and sex. The jointly nesting sandpipers display sex-dependent differences in the time spent for the prebreeding period. The exponents in allometric equations that relate duration of the prebreeding period with body weight are constant for a particular sex and differ between males and females. The time spent for prebreeding by the birds of different sexes depends on mating, parental, and territorial systems. The type of social organization of a species determines the time spent by male and female sandpipers for the prebreeding period. Relatively large-sized sandpiper species tend to reduce the calendar period for prebreeding, which imposes constraints on their social organization. Monogamy and joint parental care requires that the spatial structure of the population is more strictly controlled and retained for a longer time, thereby extending the time spent by males for this type of behavior.

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INTRODUCTION

The theory of mating systems originated from the seminal work by Darwin (*On the Origin of Species by Means of Natural Selection*), which postulated the association between sexual selection, behavioral and morphological dimorphism, as well as polygamy. However, ethologists and ornithologists since that time have mainly emphasized the specificity of species in reproductive behavior and social structure, paying little attention to individual changes in behavioral adaptability to the environment or the effect of ecological factors on specific features of individual behavior or social structure. On the other hand, Verner as early as 1964 proved in his study that mating systems were the result of the individual estimation of resources and selection (Verner, 1964). Concurrently, Crook (1964, 1965) demonstrated a correlation between the ecological structure and mating systems, and later (Crook, 1970) regarded the social structure as a dynamic system formed via the interaction of manifold ecological and social factors, emphasizing that spatial distribution and grouping trends changed within the ranges allowed by the genetic background of a species.

The empirical data accumulated so far suggest that the social systems of birds are most diverse, so that they may differ in several characteristics even in closely related species. In addition, individual populations of the same species under different conditions may differ in their social organizations, to say nothing of seasonal and time-dependent changes caused by different external and internal impacts and so on (Panov, 1983).

The first analysis of the diversity in sandpiper social organization was attempted by a team of American zoologists (Pitelka et al., 1974), who came to the conclusion that this diversity reflected both labile and conserved strategies in utilizing environmental resources. The polygamous species utilize a labile strategy. They display no nesting conservatism, freely migrate within their distribution range, and settle for breeding at the sites with the most favorable conditions during a particular season. For many of such species, the areas of defended territories vary in a wide range; therefore, they may nest with a high density in favorable sites. All monogamous sandpiper species belong to a group utilizing a conserved strategy. Characteristic of the sandpipers belonging to this group are considerable nesting conservatism, weak variation in abun-

dance, and mainly large, stable protected territories, where they find sufficient feed in any weather conditions. A pair of birds better defends their nest from predators and better protects their clutch in bad weather, since the partners can feed in turn.

The latest data confirm this general pattern. However, a deeper insight demonstrates that the social organization of some species may differ in different parts of their distribution range (Pienkowski and Green, 1976; Tomkovich and Morozov, 1983); intermediate variants between labile and conserved strategies are also frequently met.

Myers (1981) gives an alternative explanation for the differences in sandpiper social organization. He analyzed the distances between the centers of sandpiper breeding and overwintering areas and demonstrated that one of the partners of long-distance migrants, as a rule, flies away from the breeding area considerably earlier than the other, while the difference in the leaving dates of males and females for short-distance migrants is insignificant.

The importance of the fall migration period for the timing of sandpiper migration from their breeding sites and, correspondingly, for some aspects of their social organization was determined (Schneider and Harrington, 1981). It has been shown that the food resources are rapidly depleted on their main stopover areas, so that it is advantageous for sandpipers to leave their breeding sites earlier for these stopover areas. Presumably, this provides the explanation for intraseasonal differences in the participation of monogamous males and females in parental care.

Tomkovich (1984a, 1984b) notices that sandpiper species with only one of the partners involved in brooding are most diverse in southern and arctic tundras and are completely absent in polar deserts. The number of species with both partners sitting on eggs distinctly increases from the south to arctic tundras, while only monogamous species with two brooding parents enter the polar deserts. Similarly, only monogamous species inhabit the mountain tundras. Tomkovich explains this by an increase in the severity of climate from south to north, the poorness of feed resources in the polar deserts, and a dynamic distribution pattern of feeding sites in the mountains. This makes the birds leave their nests for a long time when foraging, entailing the need of alternating egg heating by male and female.

However, most researchers when studying the social organization of sandpipers have searched for the relation between mating and parental care systems, focusing on the origin of social organization (Jenni, 1974; Pitelka et al., 1974; Graul et al., 1977; Myers, 1981; Oring, 1982, 1986; Walters, 1982, 1984; Erckmann, 1983; Oring and Lank, 1984; Lenington, 1984; Tomkovich, 1984a, 1984b; Rhijn, 1985, 1990, 1991).

The durations of various phases in the breeding cycle and their relation to different sandpiper social systems has not yet been studied.

In this paper, we consider the duration of the pre-breeding period in the sandpipers nesting in northeastern Yakutia, its correlation with the sandpiper social organization, and the stability in timing of the pre-breeding period.

The birds arriving to breeding sites start the overall reproduction period and, in particular, the prebreeding period. The sandpipers nesting in the tundra zone have one of the longest migratory flyways of all birds. It is considered that the dates for sandpiper arrival to breeding areas are associated with the availability of appropriate feeds, which, in turn, depends on the appearance of thawed patches in tundra and open water at the banks of rivers and lakes (Vorob'ev, 1963, 1967; Kishchinskii, 1973a, 1973b, 1974, 1978; Kishchinskii and Flint, 1973a, 1973b; Kondrat'ev, 1979, 1982; etc.). Kondrat'ev (1979, 1982) has demonstrated that the arrival of a larger part of sandpipers mainly coincides with the period when daily average temperature exceeds zero. Evidently, other factors may also influence the arrival dates of such long-distance migrants as the tundra-dwelling sandpiper species, namely, the weather in overwintering sites and migratory flyways, the distance to cover, and degree of feed specialization of individual species. On the other hand, it has been shown for long-distance migrants that the longer the migratory flyway of a species, the more stable are the flight duration and arrival dates (Immelman, 1971; Berthold, 1980; Gwinner, 1981). A stable timing of fly progress along the migratory flyways of long-distance migrants has been also shown (Paevskii, 1962, 1967). Sema (1989) noticed that the spring timing of sandpiper flyover was stable but corresponded to a temperature range of 5–15°C.

MATERIALS AND METHODS

The work was performed at two stations of the Ornithological Unit with the Institute of Biological Problems of the North, Far East Branch, Russian Academy of Sciences in the Nizhnekolymsk raion, Yakutia, starting from May 18–20 in 1984, 1985, 1987, 1988, and 1990. In 1984 and 1985, the studies were performed on the southern shore of the Nerpich'e Lake at the inflow of the Nerpich'ya Wiska River arm and in 1987, 1988, and 1990, at the confluence of the Bol'shaya Kon'kovaya and Malaya Kon'kovaya rivers. Both biological stations are located on the left side of the Kolyma River approximately 30 and 100 km from the riverbank and approximately 45 km from the shore of the Eastern Siberian Sea. The distance between these stations is approximately 65 km. The data for both stations were pooled.

The examined sites are beyond the Arctic Circle. The polar day begins in mid-May and continues to the

Table 1. Arrival dates of some sandpiper species to the tundra of the Kolyma lowland in different years

Species	Year												
	1957*	1960*	1962*	1978**	1979**	1984	1985	1986***	1987	1988	1989***	1990	Mean
<i>C. temminckii</i>	27.05	20.05	26.05				24.05	27.05	28.05	3.06	28.05	24.05	27.5/05 ± 3.4
<i>P. pugnax</i>	26.05	21.05	27.05	25.05	23.05	26.05	26.05	28.05	28.05	3.06	27.05	24.05	27.6/05 ± 2.9
<i>G. gallinago</i>	27.05	21.05	27.05	28.05	25.05	26.05	26.05	27.05	28.05	6.06	30.05	25.05	28.4/05 ± 3.8
<i>T. erythropus</i>	27.05	29.05	29.05	25.05	23.05	28.05	31.05	27.05	28.05	6.06	26.05	25.05	28.9/05 ± 3.8
<i>C. melanotos</i>	23.05	29.05	27.05	26.05	3.06	25.05	25.05	29.05	28.05	6.06	27.05	26.05	28.1/05 ± 3.9
<i>L. griseus</i>	27.05	1.06	28.05	27.05	23.05	27.05	26.05	27.05	28.05	6.06	1.06	25.05	28.9/05 ± 3.9
<i>P. fulva</i>		29.05	27.05	25.05	24.05	27.05	26.05	28.05	28.05	3.06	3.06	26.05	29/05 ± 3.3
<i>S. squatarola</i>	27.05	28.05	29.05	24.05	23.05	28.05	1.06	27.05	28.05	3.06	3.06	26.05	29.9/05 ± 3.1
<i>C. acuminata</i>		28.05	27.05			7.06			25.05			27.05	30/05 ± 5.7
<i>P. lobatus</i>	27.05	30.05	27.05	24.05	3.06	27.05	26.05	2.06	28.05	4.06	25.05	26.05	28.6/05 ± 3.6
<i>P. fulicarius</i>	27.05	29.05	29.05	3.06	5.06	30.5	26.05	28.05	28.05	6.06	3.06	24.05	29.6/05 ± 4.2

* Vorob'ev, 1967; ** Kondrat'ev, 1982; *** E.R. Potapov and E.I. Khlebosolov (personal communications).

end of July. Thus, the sandpipers arrive during the polar day.

The date by which over 30% of the population of a certain species arrived to their nesting sites was regarded as the beginning of the prebreeding period. The end of the prebreeding period was estimated according to the beginning of incubation, using the same percentage criterion or the completion of the prebreeding period for over 90% of the population in the case of birds for which the prebreeding period was the last stage in their nesting cycle. A cumulative curve was used to determine the precise dates of mass reproduction of the studied species for a particular year. The total number of birds encountered within a radius of approximately 5 km around biological stations was taken into account in calculations.

The timing of the prebreeding period was studied for 11 sandpiper species, namely, the black-bellied plover (*Squatarola squatarola*), Pacific golden plover (*Pluvialis fulva*), spotted redshank (*Tringa erythropus*), red phalarope (*Phalaropus fulicarius*), red-necked phalarope (*P. lobatus*), ruff (*Philomachus pugnax*), Temminck's stint (*Calidris temminckii*), sharp-tailed sandpiper (*C. acuminata*), pectoral sandpiper (*C. melanotos*), common snipe (*Gallinago gallinago*), and short-billed dowitcher (*Limnodromus griseus*).

All these species nest near the biological stations, but part of these birds of various species nest farther to the north. Thus, we characterize here predominantly nesting sandpiper populations.

The social organization of sandpipers is described according to our own observations and the literature data (Kondrat'ev, 1982; Cramp and Simmons, 1983; Saether et al., 1986; Jonsson and Alerstam, 1988).

The sizes of animals are their basic characteristic and serve as a universal scale, which affects the properties of various processes, as well as various parameters

of avian biology, ecology, and energetics (Calder, 1974, 1984; Dol'nik, 1982; Schmidt-Nielsen, 1987). Evidently, the duration of the prebreeding period in the species of different sizes will also differ. Allometric analysis was used to compare the species differing in their sizes.

Any measurable characteristic of an animal will change according to a certain (dependent on body size) allometric ratio with a change in size. To find the pattern of how any studied parameter (y) changes with body size (body weight, m), a dimensionless combination is obtainable only with the help of the ratio of an increase in the measured parameter (dy) to weight. This is expressed as an allometric equation, $y = am^b$, where a determines the level of the regression line and b , its inclination. In other words, b reflects the degree of increase in the measured parameter with body weight and a , the scale of this change.

Body weight was used as the parameter characterizing the body size of a species. The body weight of 247 individuals belonging to 11 sandpiper species was measured to an accuracy of 0.1–0.5 g. In addition, we included the data of the Ornithological Unit (Institute of Biological Problems of the North) on the body weight of 336 individuals belonging to 11 sandpiper species from the same area measured in 1981–1983, 1986, and 1989. Totally, 583 sandpiper individuals were weighed. Almost all birds were weighed after shooting. The mean body weights over the reproduction season were determined for both sexes.

The dependence of the duration of the sandpiper prebreeding period on body weight was assessed using regression analysis. Combination of data dependent on the sex and social organization of individual species makes it possible to estimate the effect of social organization on the duration of the prebreeding period in sandpiper males and females.

RESULTS AND DISCUSSION

Arrival dates of sandpipers to nesting sites. Table 1 lists the dates when sandpipers arrived to the Nizhnekolym'sk raion, Yakutia. In addition to our own observations, we also involved the data by E.R. Potapov and E.I. Khlebosolov (personal communications) obtained at the same biological stations and the published results of K.A. Vorob'ev (1963) and A.Ya. Kondrat'ev (1982) for the same latitude (69° N) obtained in the sites at a distance of 30–70 km from the mentioned stations. It is evident from Table 1 that the arrival dates can be regarded as stable (the standard deviation slightly exceeds 3 days). These dates did not change from 1957 to 1990 (over 30 years of observations), despite the fact that weather conditions during this period varied.

Note that an increasingly early arrival of birds to their breeding sites has been recorded in various European countries, North Asia, and North America over the last two decades as compared with previous decades. Moreover, this pattern is observed for many species migrating not only within the continent, but also to other continents. Most researchers believe that the main reason underlying the considerable change in spring migration dates is the climate warming in the Northern hemisphere (Forchhammer et al., 1998; Brown et al., 1999; Crick and Sparks, 1999; Dunn and Winkler, 1999; Sokolov et al., 1999, 2001; Walther et al., 2002; Hubalek, 2004; Sokolov, 2006).

The studied sandpiper species were divided into four groups according to their overwintering areas described in summarized reports (Gladkov, 1951; Kozlova, 1961, 1962; Cramp and Simmons, 1983; *Migratsii ptits...*, 1985). The first group contains the species overwintering in India and Southeast Asia (Temminck's stint, ruff, common snipe, and spotted redshank); second, the species overwintering in the northern and central parts of South America (pectoral sandpiper and short-billed dowitcher); third, the species overwintering in Australia and Oceania (Pacific golden plover, sharp-tailed sandpiper, and black-bellied plover); and fourth, the phalaropes, overwintering in seas near the shores of South America. As is evident from Table 1, the first to arrive to the breeding sites are the sandpipers overwintering in India and Southeast Asia and the last, the phalaropes. Note that the arrival dates for these two groups differ in a statistically significant manner (Mann–Whitney test, $p < 0.05$). Other groups do not display statistically significant differences in their arrival dates. Nonetheless, the following trend is noticeable—the closer the overwintering areas to the breeding sites, the earlier the corresponding species arrive. The observations demonstrate that only the sandpipers of first group (shorter-distance migrants) strictly depend on weather conditions; the dates of their arrival actually vary according to the

changes in the weather in a particular year. As for the remaining groups, only adverse weather conditions cause a delay in their arrival, whereas good weather does not make them earlier. This confirms the inference that the farther a species migrates, the more stable are its flight duration and arrival dates (Immelman, 1971; Gwinner, 1975, 1981; Berthold, 1980).

Our observations show that different sandpiper species display different dependences on environmental temperature, which is associated with their foraging mode. Some species, the “short-billed”, pick their feed from the ground (Temminck's stint, pectoral sandpiper, sharp-tailed sandpiper, ruff, Pacific golden plover, and black-bellied plover); other species, the “long-billed”, feed by probing soil (common snipe, short-billed dowitcher, and spotted redshank). Phalaropes collect their food from the surface of open water. Only the short-billed species feel satisfactory at an average air temperature of 0°C. The remaining species demand positive temperatures and phalaropes additionally depend on the availability of open water and, thus, on positive daily average temperatures. Therefore, the trend of the earlier arrival of short-billed species, followed by long-billed ones, and then by phalaropes, is observed. However, this trend has a poor statistical confirmation, since the difference between the arrival dates of short-billed species and phalaropes is at the very boundary of statistical significance (Mann–Whitney test, $p = 0.055$). Nonetheless, this trend may be confirmed by another method; it is possible to divide all the sandpiper species into groups taking into account both their overwintering areas and foraging modes. In this case, only the arrival dates of the short-billed short-distance migrants differ in a statistically significant manner from the arrival dates of the phalaropes (Mann–Whitney test, $p < 0.05$), whereas the arrival dates of the long-billed short-distance migrants do not differ in a statistically significant manner.

In general, note that the short period favorable for the reproduction of the tundra sandpipers imposes stringent restrictions on the breeding period. This forces sandpipers to start reproduction as early as possible, that is, to arrive at the moment when their mere existence becomes possible. That is why sandpipers arrive to the tundra at temperatures close to critical, while they advance along the flyways in spring under more comfortable temperatures (Sema, 1989).

Different systems of sandpiper social organization do not influence their arrival dates to breeding sites, except for the phalaropes. Only in the social system of the phalaropes, females choose the sites for future nesting, thereby determining their spatial distribution. Then the female phalaropes lay eggs and fly away. In some cases, they may lay several clutches (sequential polyandry). The male phalaropes alone sit on the eggs and rear their broods. It seems rather unlikely that such a social organization is the particular factor that leads to a later arrival of these birds. The dependence

of phalarope feeding on daily average temperatures looks much more convincing.

Timing and duration of the prebreeding period of the sandpipers in northeastern Yakutia. During the prebreeding period, the male sandpipers are involved in (a) the spatial distribution of breeding birds over the area and (b) the formation of pairs. The set of behavioral patterns of this period comprises display and territorial flights, various display events on the ground, courtship, etc. In some sandpiper species (pectoral sandpiper, sharp-tailed sandpiper, and ruff), the role of males in reproduction is limited to these acts, since only females of these species sit on the eggs and rear the broods. As for other species, the contribution of males to parental care is larger but the degree of their involvement may differ. Therefore, the end of the aforementioned behavior should be regarded as the end of the prebreeding period for the male sandpipers rather than the beginning of egg incubation, although these dates may coincide in some cases.

During the prebreeding period, the female sandpipers spread over the area and form pairs, as well as develop and lay eggs. The end of egg-laying is regarded as the end of prebreeding period for the females.

The timing of the prebreeding period for different sandpiper species in the Nizhnekolym'sk raion (Yakutia) has been analyzed in different years (Table 2).

Two types of reproductive systems of the Temminck's stint have been observed in two sites. In 1985 near the Nerpich'e Lake, male Temminck's stints, after establishing the territorial structure of their sites, maintained this structure during the incubation and even part of the brood-rearing period. They made display flights and defended the sites, but did not sit on the eggs or rear broods. In the remaining years, participation of both partners in nesting was observed near the Bol'shaya Kon'kovaya and Malaya Kon'kovaya rivers. After the territorial structure of the area was established, male Temminck's stints sat on the eggs and reared their broods; correspondingly, males ceased displaying and defending their territories considerably earlier. That is why the data for the year of 1985 for the male Temminck's stints were analyzed separately from the data for the remaining years.

If we regard cessation of a certain behavioral pattern as the end of the prebreeding period rather than the beginning of incubation, then, as is evident from Table 2, the dates of the end of the prebreeding period for different sexes of the same species may considerably differ. These dates do not differ for different sexes of the same species only when the males immediately start egg-brooding (Temminck's stints in the variant with paired nesting and the phalaropes).

As has been shown, the dates for the beginning and end of the prebreeding period in different species and sexes may vary depending on the conditions in individual years. However, the duration of the prebreeding period for each species and sex is much more constant.

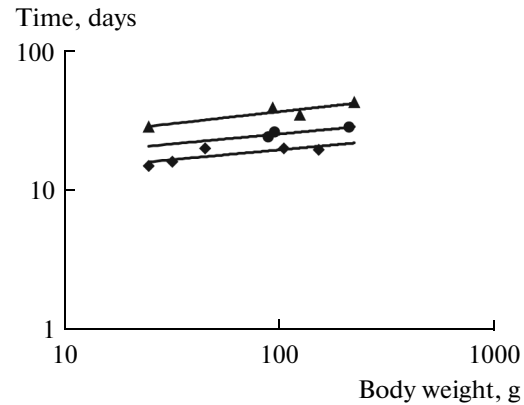


Fig. 1. Dependences of the duration of the prebreeding period on body weight for male sandpipers: triangles denote the males approximately equally involved in parental case with females; circles, males that leave the nesting sites immediately on completion of the prebreeding period and do not participate in parental care; and squares, males that either alone or almost alone incubate the clutches and rear broods.

These results suggest that the duration of the prebreeding period can be used as a species-specific and sex-dependent characteristic.

The correlation between prebreeding duration and social organization in sandpipers. Figure 1 shows how the duration of the prebreeding period of male sandpipers changes depending on their body weight. The male sandpipers form three groups of species with respect to their prebreeding behavior. The male sandpipers that incubate the eggs and rear their broods either alone or almost alone (Temminck's stint, red and red-necked phalaropes, short-billed dowitcher, and spotted redshank) are the first to complete their prebreeding behavior. The males of these species end their display and territorial flights simultaneously with the beginning of egg-brooding and cease maintaining the spatial structure of their sites. The following allometric equation describes lengthening in the prebreeding period of the males belonging to these sandpiper species with an increase in their body weight:

$$T = 10.11m^{0.14}, \quad R^2 = 66\%,$$

where T is the duration of the prebreeding period (days) and m , body weight (g).

The second group is formed of the species where the males leave the breeding sites immediately after completion of the prebreeding period and do not participate in parental care (pectoral sandpiper, sharp-tailed sandpiper, and ruff). Over the entire period in the breeding sites, the males of these species make display and territorial flights and maintain the spatial structure of their sites. The males retain this behavioral pattern almost all the time, while the females incubate the eggs and fly away just before hatching. The equation for this group is

$$T = 12.94m^{0.14}, \quad R^2 = 81\%.$$

Table 2. Duration of the prebreeding period for the sandpipers of the Kolyma lowland

Species	Year	Sex					
		males			females		
		beginning of prebreeding period	end of prebreeding period	duration of prebreeding period, days	beginning of prebreeding period	end of prebreeding period	duration of prebreeding period, days
<i>C. temmincki</i>	1985	25.05	23.06*	29*	25.05	4.06	11
	1987	28.05	10.06	13	28.05	10.06	13
	1988	3.06	20.06	16	9.06	20.06	10
	1989**	28.05	10.06	13	28.05	10.06	13
	1990	24.05	10.06	17	31.05	10.06	10
	Mean	28.05 ± 4.1	12.06 ± 5	14.8 ± 2.1	30.05 ± 5.8	10.06 ± 5.8	11.4 ± 1.5
<i>P. lobatus</i>	1984	27.05	11.06	15	27.05	11.06	15
	1985	26.05	11.06	16	26.05	11.06	16
	1987	28.05	13.06	16	28.05	13.06	16
	1988	4.06	22.06	18	4.06	22.06	18
	1989**	25.05	9.06	15	25.05	9.06	15
	1990	26.05	10.06	15	26.05	10.065	15
<i>P. fulicarius</i>	Mean	27.05 ± 3.7	12.06 ± 4.8	15.8 ± 1.2	27.05 ± 3.7	12.06 ± 4.8	15.8 ± 1.2
	1987	28.05	15.06	18	28.05	15.06	18
	1988	6.06	26.06	20	6.06	26.06	20
	1990	24.05	10.06	21	24.05	10.06	21
	Mean	29.05 ± 6.7	17.06 ± 8.2	19.7 ± 1.5	29.05 ± 6.7	17.06 ± 8.2	19.7 ± 1.5
<i>C. acuminata</i>	1984	7.06	30.06	23	7.06	22.06	15
	1987	25.05	18.06	24	25.05	10.06	16
	1990	27.05	20.06	24	27.05	11.06	15
	Mean	30.05 ± 7	22.06 ± 6.4	23.7 ± 0.6	30.05 ± 7	14.06 ± 6.7	15.3 ± 0.6
<i>C. melanotos</i>	1984	25.05	20.06	26	25.05	11.06	17
	1985	25.05	24.06	30	25.05	10.06	16
	1987	28.05	23.06	26	28.05	10.06	13
	1988	6.06	27.06	21	6.06	17.06	11
	1989**	27.05			27.05	9.06	13
	1990	26.05	20.06	25	26.05	8.06	13
<i>G. gallinago</i>	Mean	28.05 ± 4.6	22.06 ± 2.9	25.6 ± 3.2	28.05 ± 4.6	10.06 ± 3.2	13.8 ± 2.2
	1984	26.05	3.07	38	27.05	12.06	16
	1985	26.05	4.07	39	26.05	12.06	15
	1987	28.05	4.07	37	28.05	14.06	17
	1988	6.06	14.07	38	6.06	23.06	17
	1990	25.05	3.07	39	25.05	11.06	17
<i>L. griseus</i>	Mean	28.05 ± 4.9	5.07 ± 4.7	38.2 ± 0.8	28.05 ± 4.8	14.06 ± 4.9	16.4 ± 0.9
	1984	27.05	17.06	21	27.05	6.06	10
	1985	26.05	17.06	22	26.05	5.06	10
	1987	28.05	15.06	18	28.05	5.06	8
	1988	6.06	24.06	18	6.06	14.06	8
	1989**	1.06			1.06	8.06	7
<i>P. pugnax</i>	1990	25.05	13.06	19	25.05	4.06	10
	Mean	29.05 ± 4.5	17.06 ± 4.1	19.6 ± 1.8	29.06 ± 4.5	7.06 ± 3.7	8.8 ± 1.3
	1984	26.05	23.06	28	26.05	5.06	10
	1985	26.05	28.06	33	26.05	5.06	10
	1987	28.05	23.06	26	28.05	6.06	9
	1988	3.06	27.06	24	6.06	16.06	10
<i>P. pugnax</i>	1989**	27.05			27.05	6.06	10
	1990	24.05	20.06	27	24.05	3.06	10
	Mean	27.05 ± 3.4	24.06 ± 3.3	27.6 ± 3.3	28.05 ± 4.6	6.06 ± 4.6	9.8 ± 0.4

Table 2. (Contd.)

Species	Year	Sex					
		males			females		
		beginning of prebreeding period	end of prebreeding period	duration of prebreeding period, days	beginning of prebreeding period	end of prebreeding period	duration of prebreeding period, days
<i>P. fulva</i>	1987	28.05	2.07	35	28.05	7.06	10
	1988	6.06	8.07	32	6.06	17.06	11
	1989**	3.06			3.06	15.06	12
	1990	26.05	30.06	35	26.05	5.06	11
	Mean	31.05 ± 5.1	3.07 ± 4.2	34 ± 1.7	31.05 ± 5.1	11.06 ± 5.9	11 ± 0.8
<i>T. erythropus</i>	1985	31.05	18.06	18	31.05	8.06	8
	1987	28.05	15.06	18	28.05	6.06	9
	1988	6.06	28.06	22	6.06	18.06	12
	1989**	26.05			26.05	4.06	9
	1990	25.05	13.06	19	25.05	3.06	10
	Mean	29.05 ± 4.8	18.06 ± 6.7	19.3 ± 1.9	29.05 ± 4.8	7.06 ± 6	9.6 ± 1.5
<i>S. squatarola</i>	1984	28.05	10.07	43	28.05	10.06	13
	1985	1.06	13.07	42	1.06	13.06	12
	1987	28.05	10.07	43	28.05	9.06	12
	1988	3.06	13.07	40	3.06	14.06	11
	1989**	3.06			3.06	15.06	12
	1990	26.05	4.07	41	26.05	6.06	11
	Mean	30.05 ± 3.4	10.07 ± 3.7	41.8 ± 1.3	30.05 ± 3.4	11.06 ± 3.4	11.8 ± 1.8

* Different systems of social organization (see text for details); ** E.R. Potapov, personal communication

The last to end their prebreeding behavior are the species where the males and females are equal contributors to parental care (common snipe, Pacific golden plover, and black-bellied plover). The males of these species continue their display and territorial flights during the overall period of incubation. They either participate in the egg-brooding (Pacific golden plover and black-bellied plover) or do not (common snipe); later, both partners rear their broods. This group also includes the Temminck's stint, the males of which defend their sites until hatching. The equation for this group is

$$T = 17.85m^{0.15}, \quad R^2 = 82\%.$$

The exponents in equations for these groups do not differ in a statistically significant manner, thereby suggesting a general pattern of the increase in prebreeding duration, depending on the body weight for the male sandpipers within different groups. The total level of time expenditures is determined by the type of sandpiper social organization. In comparable units, the males of the third group spend 1.77-fold and 1.38-fold more time on prebreeding behavior as compared with the males belonging to the first and second groups, respectively, and the males of the second group, 1.28-fold more time than the males of the first group. The main factors when assessing the duration of the prebreeding period are the territorial and display behavior, and the behavior itself has emerged to be strictly correlated to the mating and, especially, parental care systems.

Earlier, the studies of the spatial structure of sandpiper populations revealed different opinions on the ecological significance of the defended territory as well as territorial and display behavior patterns (Holmes, 1966, 1970; Kishchinskii, 1974; Pitelka et al., 1974; Flint and Tomkovich, 1978; Hilden, 1979; Kondrat'ev, 1982; Tomkovich and Fokin, 1984). According to one view, the protected territory, as well as the display and territorial flights, serve for attracting the partner, while the area of the territory has no functional significance. According to the other, the area of this territory is determined by the ability of adult individuals to survive there at the beginning of nesting. According to the third hypothesis, the territorial behavior provides for limiting the number of broods and their spatial distribution (Khlebosolov, 1984, 1985, 1986).

By the case study of sandpipers nesting in north-eastern Yakutia, we see that once both partners are involved in parental care, the population spatial structure is maintained until hatching. In other words, new birds are prevented from settling in the used area. This provides for a decrease in competition for feeding grounds between both the adult birds and broods. If male sandpipers do not participate in incubation and brood rearing, they fly away from the tundra long before hatching and continue their territorial and display behavior while still staying there. In this case, new birds, for example, females with broods, can settle in

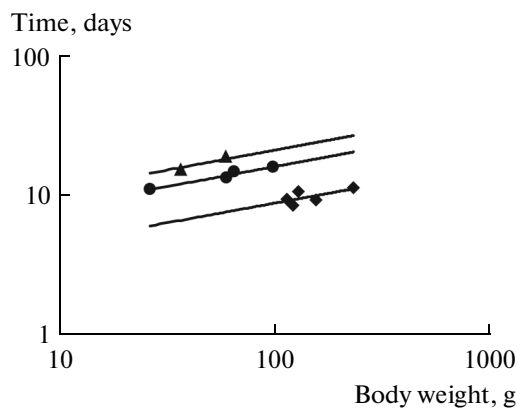


Fig. 2. Dependences of the duration of the prebreeding period on body weight for female sandpipers: triangles denote the females involved in territorial distribution and securing of individual sites for nesting pair; circles, females that mate directly on nesting sites; and squares, females that arrive to the breeding areas together with males either in formed pairs or within migrating mating groups.

the already occupied area; however, this settling takes place 5–7 days after the first egg-laying. A decrease in the competition between broods is attained by either spatial or temporal separation. However, when males incubate the clutch and rear their broods either alone or predominantly alone, they stop their display and territorial behavior with the beginning of incubation. In this case, new birds also can settle in this territory; however, the age difference between broods will also amount to 5–7 days due to the time of egg-laying. Correspondingly, the situation with broods will be the same as in the previous group. This suggests that the main function of display and territorial behavior is spatial distribution, while attraction of a mate is an accompanying function.

Figure 2 shows how duration of the prebreeding period for female sandpipers changes depending on their body weight. For all females, the end of egg-laying may be regarded as the end of the prebreeding period. The trend of a shorter calendar prebreeding period for larger-sized species is evident from Fig. 2. This trend is describable with a general equation (not shown in Fig. 2):

$$T = 28.62m^{-0.18}, \quad R^2 = 21\%.$$

However, the statistical significance of this equation is not high and can be considerably increased by dividing all the data taking into account the social organization of species.

For the female sandpipers, it is reasonable to form three groups of species based on their social organization. The first group unites the species, in which the females arrive to nesting sites jointly with males either as formed pairs (short-billed dowitcher, Pacific golden plover, spotted redshank, and black-bellied plover) or within migrating mating groups (ruff). These females

spend no time on mating and are first to start nesting. The equation for this group is

$$T = 2.54m^{0.28}, \quad R^2 = 47\%.$$

The second group comprises the species where the females establish mating relations directly on nesting sites (Temminck's stint, pectoral sandpiper, sharp-tailed sandpiper, and common snipe). The equation for this group is

$$T = 4.51m^{0.28}, \quad R^2 = 96\%.$$

The third group includes the red and red-necked phalaropes. Unlike the former two groups, the females of these species take on the functions of spreading over the territory and securing individual sites for the nesting pair; therefore, their prebreeding period is longer as compared with the females from the other groups. In a comparable form, this equation may be put down as

$$T = 5.91m^{0.28}.$$

The exponents in equations for these groups do not differ in a statistically significant manner, demonstrating a general pattern within the groups of an increase in the duration of the prebreeding period of female sandpipers with their body weight. Similar to male sandpipers, the time spent by females on the prebreeding period is determined by the type of their social organization in each group of species. In comparable units, the female phalaropes spent 2.33-fold and 1.31-fold more time for the prebreeding behavior as compared with the females from the first and second groups, respectively, which may be regarded as the cost for the function of spatial distribution. The females of the second group spent 1.78-fold more time than the females of the first group, which may be regarded as the cost for the search of an appropriate mate.

Bird nesting under northern conditions with a short period favorable for reproduction imposes restrictions on the reproductive season. Since the total duration of the reproductive period increases with body size, owing to a strict correlation of various bird biological and physiological parameters with their body weight, large-sized species may encounter a deficiency in the time for breeding. Therefore, relatively large-sized sandpiper species tend to reduce the calendar time for the prebreeding period. This is possible by shifting part of behavioral events, namely, the establishment of pairs, to the periods of migration or overwintering. In turn, this entails a different social organization of large-sized species as compared with smaller-sized ones. Monogamy and parental care involving both partners are much more frequent among large-sized sandpiper species.

The relation between sandpiper mating and parental systems has been repeatedly discussed. It has been shown that monogamous species are inclined towards joint parental care, whereas polygamous species, towards an individual care. Note that in the polyandrous species, males as a rule are involved in parental care, versus females in the case of polygynous species. However, this is a well-pronounced trend rather than a

correlation (Jenni, 1974; Pitelka et al., 1974; Graul et al., 1977; Myers, 1981; Oring, 1982, 1986; Walters, 1982, 1984; Erckmann, 1983; Lenington, 1984; Oring and Lank, 1984; Rhijn, 1985, 1990, 1991). On the other hand, monogamy and joint parental care lead to the need of more stringent control and maintenance of the population spatial structure, thereby increasing the time expenditures of males on such behavioral pattern.

The exponents in the equations describing the prebreeding period duration for females are closest to the exponents in the dependences of their maximum lifespan on body weight (Gavrilov, 1994, 1995). Presumably, this is to the largest degree determined by physiological processes and is associated with the duration of egg development. The exponents in the equations describing the prebreeding period duration for sandpiper males are approximately twofold smaller as compared with the females.

Thus, sandpipers start their reproduction as early as possible and arrive at the tundra at temperatures close to critical. The dates for the beginning of reproduction depend on the foraging mode and the distance to overwintering sites. The duration of the prebreeding period is constant for each species and sex. The timing of the prebreeding period of jointly nesting sandpipers displays sex-related differences. The exponents in the allometric equations for the dependence of the prebreeding period duration on bird body weight are constant for the particular sex and differ between males and females. The time spent by different sexes for the prebreeding period depends on the mating, parental, and territorial systems. In other words, the type of social organization of a species determines the time spent by male and female sandpipers for the prebreeding period. The relatively large-sized species tend to reduce the calendar duration of the prebreeding period, which imposes restrictions on their social organization. Monogamy and joint parental care entail the need for more stringent control over the population spatial structure and its longer retention, thereby increasing the time spent by males on such behavior.

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