Migration of Curlew Sandpipers *Calidris ferruginea* in southern Central Siberia

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Curlew Sandpiper studies were undertaken in southern Central Siberia over the period 1980–2003. Most records on northward migration were in the final decade of May and early June; few birds were recorded. The peak of southward migration for adults was 16–25 July, and for juveniles was 20 August–4 September. As many as 20,000 birds could be in the region at the time of peak migration of juveniles, and the total number of Curlew Sandpipers on southward migration in years of successful breeding is estimated as being at least 35,000–40,000 birds. Migration was on a wide front, across the entire region. On southward migration, stopover duration averaged 5.3 days for adults 3.8 days for juveniles; birds concentrated on the steppe lakes and seldom occurred on water bodies in the taiga zone. The average rates of body mass gain was 4.1 g per day in adults and 1.2 g per day in juveniles. In adults, no moult was recorded for primaries or remiges, but most adults were migrating with body feather tracts in moult, and the moult of males was slightly more advanced than females. No moult was found in juveniles. The breeding grounds of Curlew Sandpipers on passage through the region are not known; ring recoveries provide migratory links with Australian nonbreeding grounds.

INTRODUCTION

The southern part of Central Siberia includes the central and southern portions of Krasnoyarsk Region, as well as the Khakasia and Tuva Republics. It covers an extensive territory between the Sym River (60°30'N, 88°30'E) on the Yenisey Plain in the north and the Ubsu-Nur Lake (50°35'N, 93°00'E, Ubsu-Nur Depression) at the border between Tuva Republic and Mongolia to the south. This area embraces several natural zones; from north to south these are taiga, subtaiga, forest-steppe, steppe, arid steppe and also includes mountains in the south.

The climate of this region is determined by its location in the heart of the Asian continent, and the consequent peculiarities of atmospheric circulation and geographical features. Due to the remoteness from oceans, the climate is sharply continental, especially in the southern part of the region. A characteristic feature is the western "transfer", a wind that dominates throughout the year around at altitudes of 1,000–2,000 m. Alpine relief determines a wide diversity of local climate conditions. From late March to early May, unstable weather occurs, and temperature fluctuations reaching tens of degrees are common. In summer the Front-Asian thermal depression forms in the south of the region, and cyclone activity occurs. Autumn is short, with sunny, dry weather and a gentle breeze. Night frosts start in September but occasionally occur in August (Modern Climate of the Ecoregion, 2001).

Prior to this study, information about the occurrence of Curlew Sandpipers *Calidris ferruginea* in southern Central Siberia annually on passage was limited to Tugarinov & Buturlin (1911), Sushkin (1914, 1938), Yanushevich (1952), Kozlova (1962) and Rogacheva (1992). These suggested that the species was irregular both spatially and temporally. Since 1980, our studies have been based mostly on the wetlands of southern Central Siberia which seemed to be the main staging sites for migrant waders in the region. This paper leads to a reassessment of the status of the species in the region, and provides new information about distribution, numbers, dates of migration, moult, dynamics of body mass, and sex and age structure of Curlew Sandpipers. Information from ring recoveries helps to determine migratory links of birds passing through the region.

STUDY AREA AND METHODS

Our studies were carried out between 1980 and 2003 at sites in southern Central Siberia; in 1991 we visited the Irkutsk-Cheremkhovskaya Plain, west of Lake Baikal (Fig. 1, Table 1). The main staging sites and concentrations of waders and waterfowl in the southern Central Siberia are listed in Table 1 excluding Irkutsk-Cheremkhovskaya Plain which geographically belongs to the Baikal Lake region. (Wetlands in Table 1 which are not mentioned further in the text did not have Curlew Sandpipers recorded during this study.)

Data collected at field stations used standard methods for studies of bird migrations (Savchenko 1991a), and were conducted by the staff of the Krasnoyarsk State University (KrasSU). We made sight records, did transect counts on foot and from boats and vehicles. We trapped birds for ringing, and made standard observations of birds in the hand. Statistical analysis of directional data on migration followed Batschelet (1965).

Trapping and ringing were undertaken mainly during July to September from 1980 to 2000; in 1983 and 1987 we trapped continuously between 20 April and 14 September at Khadyn Lake. Catching was conducted throughout the day using (1) standard mist nets (15 × 2.5–3.0 m with mesh of 18–30 mm), (2) nets of size 25–30 × 3.5–4.0 m with mesh 40–50 mm, and (3) portable wire cage traps (45 × 25 × 6–7 m). The nets were set up perpendicular to the shoreline of a wetland. A combination of these three catching methods was

used in a uniform complex (Savchenko 1991b). All birds were fitted with a metal ring as well as colour plastic rings; in early years (1980–1984) neck-ties were applied instead of colour rings. In total we ringed 1,136 Curlew Sandpipers among 15,267 waders.

Bill length was not measured in captured birds, it was measured only in collected specimens. As a result data on sex ratio during migration are fragmentary. During wader trapping in Khakasia it was not feasible to weigh all birds; limited data on Curlew Sandpipers of known sex, age and mass are therefore mostly based on specimens in the Zoological Museum of KrasSU. Body mass was measured mostly at Khadyn Lake during southward migration in 1982, 1984 and 1987 to 0.1 g. During processing wing lengths were measured (maximum chord to 1 mm) and fat was scored according to the five-point scale of Dol'nik (1975).

Moult of adult Curlew Sandpipers was recorded both in museum specimens and in the field during ringing activities on southward migration during the period from 16 July to 25 August in 1984 at Khadyn Lake. The study period covered the entire passage of adults in the study area. Stages of feather growth and intensity of moult were described according to

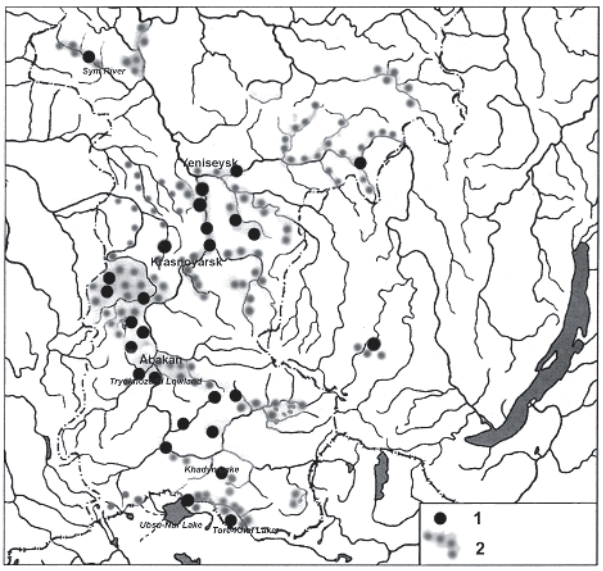

Fig. 1. Sites of studies of Curlew Sandpiper in Central Siberia in 1980–2003: 1 – stationary studies, 2 – routes of transect counts by foot, by boat or car.

Table 1. Areas and years of studies of Curlew Sandpiper migration in southern Central Siberia.

Area	Coordinates	Years
Ubsu-Nur Depression		
Ubsu-Nur Lake (Tuva)	50°35'N, 93°00'E	1980
Tore-Khol Lake (Tuva)	50°03'N, 95°00'E	1980, 1982, 1989
Foothills of West Sayan		
Chaa-hol Village (Tuva)	51°40'N, 92°20'E	1982
Central-Tuva Depression		
Khadyn Lake (Tuva)	51°20'N, 94°30'E	1980, 1982, 1983, 1984, 1987, 1988, 1989, 1991, 2000
West Sayan Range		
Oiskoye Lake (Krasnoyarsk Region)	52°50'N, 93°15'E	1989–1990
Khut River (Krasnoyarsk Region)	52°40'N, 93°35'E	1991
Gagulskaya Depression (Krasnoyarsk Region)	52°00'N, 93°00'E	1990
Southern-Minusinsk Depression		
Tryokhozerki Lowland (Khakasia)	53°20'N, 91°30'E	1990, 1991, 1997–2003
Sorokaozerki Lowland (Khakasia)	53°20'N, 91°15'E	1986
Ulug-Kol Lake (Khakasia)	53°48'N, 90°35'E	1986, 1989, 2003
Foothills of Kuznetsky Alatau Range		
Abakan River (Khakasia)	53°00'N, 90°20'E	1985, 1986, 1990
Chulym-Yenisey Depression		
Bele Lake (Khakasia)	54°40'N, 90°10'E	1985, 1987, 1997
Intikol Lake (Krasnoyarsk Region)	54°57'N, 90°35'E	1990, 1999, 2003
Gorkoye Lake (Khakasia)	54°35'N, 90°55'E	1991, 1999, 2000, 2003
Salbat Lake (Krasnoyarsk Region)	55°12'N, 89°36'E	1991, 2003
Central Yenisey		
Travyanoy Island (Krasnoyarsk Region)	56°35'N, 93°45'E	1988
Pavlovshchina Village (Krasnoyarsk Region)	56°45'N, 93°35'E	1989, 1991
Makrushinskoye Village (Krasnoyarsk Region)	57°31'N, 93°15'E	2001, 2002
Kansk forest-steppe		
Aban River (Krasnoyarsk Region)	56°38'N, 95°45'E	1998
Noshinsky Pond (Krasnoyarsk Region)	57°02'N, 95°24'E	2000
Lower Angara		
Motiginskiye Isles (Krasnoyarsk Region)	58°10'N, 94°34'E	1994
Yenisey Plain		
Sym River (Krasnoyarsk Region)	60°30'N, 88°30'E	1997, 1999, 2002
The area west of the Baikal Lake Irkutsk-Cheremkhovskaya Plain (Irkutskaya Oblast)		
Kirey River	54°20'N, 100°00'E	1989
Iya River	54°45'N, 100°30'E	1989

Vinogradova *et al*. (1976) and were adapted to the feather scoring system of Western Europe: 0: old feather, 1: old feather is missing or a new one is completely covered with the sheath, 2: new feather is emerging from the sheath up to 1/3 grown, 3: between 1/3 and 2/3 of feather length is free of sheath, 4: more than 2/3 of feather length is free of sheath, 5: new feather without sheath. Specimens in Zoological Museum of KrasSU were used primarily for tracking changes in colouration of contour feathers and to a lesser degree for quantitative assessments of feather growth because scoring the moult of feathers is more difficult in dry specimens than in live or freshly dead birds.

Sexing was carried out by examination of gonads at skinning of specimens. Adults and juveniles (first year birds) were separated on plumage characteristics.

Along with studies at field stations (Table 1) counts of birds on transects were carried out in various years in Nazarovo Depression (Bolshoy Kosogol and Maly Kosogol Lakes, Serezh River), Kansk Depression (Ulyukol Lake and Usolka River), in South-Minusinsk Depression (Potaga, Nalivnoye, Dzhirimskoye Lakes and other smaller ones), in the valley of the Yenisey and its left tributaries. In total over 3,000 km were covered on foot during transect counts. These counts are presented as numbers of birds per 10 km of a shoreline. Aerial surveys of water bodies throughout southern Central Siberia were undertaken in 1986–1991 to detect concentrations of waterbirds.

RESULTS

Status

The Curlew Sandpiper was a common, sometimes abundant species during both northward and southward migration (Fig. 2); abundance varied greatly between years. In the Tuva Republic, Curlew Sandpipers on southward migration were classified as being either abundant or rare. For example, it was the third most abundant species in Central-Tuva Depression in 1982 and 1984 and comprised 11% of the total catch of sandpipers (Savchenko 1986), but in 1988 and 1989 only a few solitary birds were ringed there. On average, this species comprised 6.1% (SD 2.3%) of the number of *Calidris* waders trapped over five years. In Khakasia Republic, Curlew Sandpipers accounted on average for 35.1% (SD 6.0%) of *Calidris* waders over six years; in 1986, 1990 and 1991 the percentage in catches exceeded 45%.

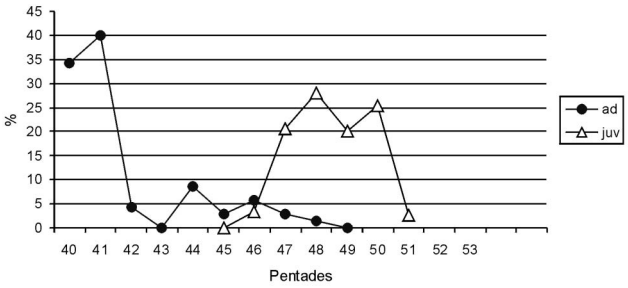

Fig. 2. Dynamics of abundance of Curlew Sandpipers at Khadyn Lake, Central-Tuva Depression, in catches in 1984 (*n* = 220 birds).

Phenology of migration

Information about the presence of Curlew Sandpipers in southern Central Siberia during northward migration was limited (Table 2) and suggested that northward migration lasted approximately 15 days and that there were differences in dates of migration within the region. Difference in the starting dates of migration between Ubsu-Nur and Central-Tuva Depressions was 5–7 days, while migration in the latter and Minusinsk Depression started simultaneously in spite of presence of dividing snow-covered ridges of the Sayany Mountans in late May. Farther north, at the latitude of Krasnoyarsk, Curlew Sandpipers were usually present in early June.

Records during the period between northward and southward migrations were rare; single birds were recorded twice during our studies in Khakasia: on 26 June 1991 at Trekhozerki Lowland and on 1 July 2000 at Bele Lake.

Southward passage started in early July; the first sight records were made on 7–9 July (Table 3), and in catches they occurred from 15–16 July. The latest date on which an adult Curlew Sandpiper was recorded was 27 August 1982 (Table 4). Juveniles were observed and caught during the period from 7 August till 23 September (Table 4).

The overall period of southward passage lasted 79 days: 52 days in adults and 48 days in juveniles. The intensity of migration was not uniform during the period of southward passage (Fig. 2). Adults were most abundant during the period from 16 to 24 July 1984 and between 17 and 25 July 1987 at Khadyn Lake. The peaks for juveniles at Khadyn Lake were 23 August–2 September 1982 and 20 August–4 September 1984.

Table 2. Dates of records during northward migration of Curlew Sandpipers in southern Central Siberia: n.d. = no data; * = V.I.Yemelyanov pers. comm.; ** = Kozlova (1962).

Area	Year	Date	Number of birds
Tuva			
Ubsu-Nur Lake, Ubsu-Nur Depression	1982	23 May–30 May	25
Tore-Khol Lake *	1989	22 May–29 May	8, 5, 15
Khadyn Lake, Central-Tuva Depression	1983	30 May, 1 June	2, 8
	1987	28 May	2
Khakasia			
Trekhozerki Lowland, Minusinsk Depression	1991	28 May, 1 June	small groups
Bele Lake, Chulym-Yenisey Depression	1991	27 May	5
Abakan steppe **	1962	15 June	n.d.
Krasnoyarsk Region			
Pavlovshchina Village, Yenisey River	1991	5 June	1 male, 1 unsexed
Krasnoyarsk (vicinity)	1983	29 May–5 June	5
Sewage farm of Sosnovoborsk	1998	2 June	6
	2000	3 June	5, 4

Density and abundance

Although Curlew Sandpipers were not numerous on northward migration, the density of this species on some wetlands of Tuva (Tore-Khol Lake) and Khakasia (Trekhozerky Lowland, Gorkoye Lake) reached 30–40 birds/10 km of shoreline. In Trekhozerky Lowland on 28 May 1991, 44.3 birds/10 km were recorded; four days later the density had decreased to 20.0 birds/10 km.

During southward migration, especially when juveniles were on passage, Curlew Sandpipers occurred on a large number of water bodies. Substantial concentrations were limited to a small number of water bodies with favourable ecological conditions; judging by bird movements between years such conditions did not remain constant at the same lakes. Thus, on the southern coast of Khadyn Lake (Tuva) in excess of 1,000 birds/10 km were recorded in 1982, but only 25–50 in 1989. At Gorkoye Lake (Khakasia), 950–1,100 Curlew Sandpipers were present on 18–28 August 1999 on an area of 3.5 km^2, but only 100–150 Curlew Sandpipers during this period in 2000. In Trekhozerky Lowland mean density was 196 birds/10 km between 4 August and 4 September 1991; over the following 10 days, it decreased to 25.7 birds/10 km. Densities (birds/10 km, the range over all years for which data were available) were recorded at other water bodies during southward migration: 60–80 in South-Minusinsk Depression, west of Yenisey (Ulug-Kol, Potaga, Uskol, Nalivnoye and other lakes); 1–18 in South-Minusinsk Depression, east of Yenisey (Tagarskoye Lake and others); 90–150 in Chulym-Yenisey Depression (Intikol, Dzhirimskoye, Bele, Shira and other lakes); 10–15 in Nazarovo Depression (Beloye, Bolshoy and Maly Kosogol Lakes, floodplain of Serezh River); 17–65 on wetlands of Kansk forest-steppe (Noshino pond, Usolka River and Ulukol Lake).

Counts of Curlew Sandpipers recorded on the main wetlands of southern Central Siberia on southward migration suggested a total of at least 20,000 birds simultaneously (Table 5).

Table 3. Dates of southward migration of Curlew Sandpipers in southern Central Siberia based on occasional observations: n.d. = no data; * = Tugarinov & Buturlin (1911); ** = V.I. Yemelyanov (pers. comm.).

Area	Year	First record	Mass migration	Last record
Krasnoyarsk region				
Krasnoyarsk District *		first third of July	n.d.	till mid-August
Bolshoy Kosogol and Maly Kosogol Lakes, Nazarovo Depression	1991	n.d.	20 August–2 September	12 September
Beloye Lake			25 August	12 September
Intikol Lake, Chulym-Yenisey Depression	1990	15–16 July ad	26 July–30 August	8 September
	1991	11 July ad	n.d.	5 September
	1996	15 July	n.d.	n.d.
Noshino pond, Kansk Depression	1991	n.d.	22 August	7 September
Tagarskoye Lake, east of Yenisey	1991	n.d.	16 August	n.d.
Amyl River, Foothills of Western Sayany Mountains**	2001	n.d.	18–20 August	n.d.
Lebedevsky pond, Karatuz steppe **	1995	n.d.	3.08	n.d.
Khakasia				
Ulug-Kol and Potaga Lakes, Uibat steppe	1986	14–16 July ad	25 August–2 September	10 September
	1993	9 July ad**	24 August	n.d.
	1995	11 July ad	n.d.	n.d.
Dzhirimskoye Lake, Chulym-Yenisey Depression	1991	7 July ad**	21 August	n.d.
Tuz Lake	1996	n.d	30 August	n.d.
Tuim River	1996	n.d.	30 August	n.d.
Trekhozerky Lowland, Koibalskaya steppe	1991		4 August–4 September	

Table 4. Dates of southward migration of Curlew Sandpipers in southern Central Siberia based on observations at field stations: – = no phenomenon; n.d. = no data; ** = Tolchin & Pyzhyanov (1980).

Area	Year	First record		Mass migration		Last record	
		ad	juv	ad	juv	ad	juv
Tuva							
Khadyn Lake, Central-Tuva Depression	1982	n.d.	n.d.	n.d.	23 August–2 September	27 August	23 September
	1984	15 July	17 August	16–24 July	20 August–4 September	26 August	13 September
	1987	16 July	7 August	17–25 July	7–28 August	27 August	13 September
	1988	n.d.	9 August	–	19 August	21 August	17 September
	1989	n.d.	–	–	–	–	10 September
Khakasia							
Koybalskaya steppe, Trekhozerky Lowland	1990	n.d.	8 August	–	27 August–2 September	19 September	21 September
Uskol Lake, Uybatskaya steppe	1990	n.d.	8 August	n.d.	n.d.	n.d.	n.d.
Trekhozerky Lowland	1991	n.d.	7 August	–	14 August–8 September	5 September	13 September
Gorkoye Lake, Chulym-Yenisey Depression	1999	n.d.	n.d.	–	26 August–?	–	n.d.
Bele Lake, Chulym-Yenisey Depression	1985	n.d.	9 August	–	17–22 August	20 August	n.d.
Minusinsk Depression**		n.d.	n.d.	n.d.	1–9 September	n.d.	n.d.

Curlew Sandpiper migration occurred on a wide front, from the western to eastern borders of southern Central Siberia. During southward migration birds concentrated on the steppe lakes of the region. Curlew Sandpipers occurred rarely on water bodies in the taiga zone and the taiga belt in mountains. The Yenisey River did not appear to provide a general directing line for migration; however, under favourable conditions Curlew Sandpipers stopped on shores of the river and its reservoirs.

Variation of numbers of Curlew Sandpipers between years on wetlands of the region is reflected in catches for ringing (Table 6). However, it should be taken into account that catching activities were limited in time in 1986 and 1999. It can be supposed that this variation reflects fluctuation in breeding success of birds. However, it seems that the observed fluctuations in numbers did not always reflect species breeding success correctly, even when obtained on a single water body as large as Khadyn Lake.

Figure 3 shows fluctuations in numbers of migrating and breeding waders at Khadyn Lake, together with two parameters of water table state (these certainly reflect ecological conditions) during 13 years of observations. A distinct negative correlation occurs between shoreline level and size of mudflats; a drop of water level always (apart from 1983) led to formation of extensive mudflats. The latter event was followed by increases of numbers of staging migrant sandpipers. The peak abundance of Curlew Sandpipers was recorded in 1982 when mudflats were most extensive and

Table 5. Maximum numbers of Curlew Sandpipers, simultaneously staging on different wetlands of southern Central Siberia on southward migration.

No. of wetland	Area, wetland	Abundance of individuals
1	**Ubsu-Nur Depression (Tuva):** Ubsu-Nur Lake	250
2	Tore-Khol Lake	350
3	Shara-Nur Lake (Sharanursko-Dus-Kholsky wetland complex)	550
4	**Foothills of Western Sayany Mountains:** Chaa-Khol Village, Sayanskoe reservoir	150
5	Wetlands of Uyuk Depression	350
6	**Central-Tuva Depression:** Khadyn Lake	2,500
7	Cheder Lake	1,100
8	Kak-Khol Lake	1,200
9	**Western Sayany Mountains:** Oyskoye Lake	25
10	Khut River	45
11	Wetlands of Gagul Depression	45
12	Tyukhtet-Shadatsky wetland complex	350
13	**Water bodies of East Tuva Upland:** Myun-Khol Lake	950
14	Tere-Khol (Kungurtug) Lake	350
15	**South-Minusinsk Depression:** Trekhozerky Lowland and Bugayovo Lake	1,900
16	Sorokaozyorky Lowland	350
17	Ulug-Kol Lake and shallow lakes of Uibat steppe	650
18	Bidzhinsk puddles, sewage farm and amelioration system in Abakan steppe	450
19	Krasnoye Lake	120
20	**Right bank part of Minusinsk Depression (east of Yenisey):** Tagarskoye Lake	120
21	Tubinsky Bay of Krasnoyarsk reservoir	350
22	Bolshoy Kizikul and Maly Kizikul Lakes	75
23	**Chulym-Yenisey Depression:** Bele and Sukhoy Itkul Lakes	1,200
24	Shira Lake	550
25	Tuz Lake and adjacent lakes in the area of Solonoozernoye Village	250
26	Intikol Lake	350
27	Tolsty Mys Lake	150
28	Gorkoye Lake	1,100
29	Salbat Lake	50
30	Saragashsky and Sydinsky Bays of Krasnoyarsk reservoir	250
31	Dzhirim Lake	150
32	**Nazarovo Depression:** Kandatskoye reservoir	50
33	Beloye and Gusinoye Lakes	150
34	Bolshoy Kosogol Lake	50
35	Mikhaylovsky pond	75
36	Krutoyarsky pond	75
37	Serezh River	50
38	**Middle Yenisey River:** Travyanoy Island	50
39	Pavlovshchina and Yukseevo Villages	150
40	Makrushinskoye Village	25
41	Sewage farm of Sosnovoborsk	450
42	Kansk forest-steppe: **Aban River**	**100**
43	Noshinsky pond	350
44	Taray Lake	50
45	Lower Angara River: **Motiginsky Isles**	**150**
46	**Middle Angara River:** Kezhma Isles	250
47	**Yenisey Plain:** Sym River	25
	Total	**18,330**

Table 6. The numbers of Curlew Sandpipers ringed in Tuva and Khakasia republics.

	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1999	Total
Tuva	118	0	220	–	–	21	24	2	–	–	–	385
Khakasia	–	–	–	243	9	–	–	2	162	302	26	744

ecological conditions probably optimal. Low numbers were recorded both when mudflats dried out and when these feeding areas were flooded when the water table was high (for example, in 1985 and 1986). The year 1989 was the only exception; juvenile Curlew Sandpipers were totally absent.

In 1988 adult Curlew Sandpipers did not stop at Khadyn Lake, probably as a result of unfavourable ecological conditions on the lake, and the almost total absence of adults and the total absence of juveniles in 1989 can be attributed to the combined effect of unfavourable ecological conditions on both the lake and the breeding grounds.

Age composition

During long-term catching and ringing of birds during southward migration at Khadyn Lake, Tuva Republic, juvenile Curlew Sandpipers started to predominate numerically over adults from the 47th pentade (20–24 August) onwards (Table 7). Adults migrated before juveniles, starting from the 39–40th pentades (16–20 July). In September only juvenile Curlew Sandpipers were caught. Juvenile birds predominated numerically both in Tuva and Khakasia republics. For example, at Khadyn Lake they formed 68.2% in 1984 and 63.2% in 1987; at Trekhozerky Lowland 99% in 1990 and 92% in 1991 (Table 7 & 8). At Gorkoye Lake only juvenile Curlew Sandpipers were present on 26–28 August 1999.

Sex composition

On northward migration, two adult males and two adult females were collected on 27 May 1989 at Tore-Khol Lake, Tuva Republic and one adult male on 5 June 1991 at Pavlovshchina Village on the Yenisey River, Krasnoyarsk Region. On southward migration, nine adult males and six females were captured at Khadyn Lake on 5–20 July 1984 and two males and six females in the following 5-day period (21–25 July). This means that at least in some years percentage of females can be rather high even at the beginning of southward migration. Adult males are thought to start southward migration ahead of females. In first-year birds no difference in dates of migration was found between sexes: males were captured on 17 and 28 August, and 3 September; females on 31 August and 2 September.

Moult

No moult was found in juveniles, therefore the following description deals with adults on southward migration only. In adults neither primaries, nor remiges nor the smaller wing feathers were in moult, whereas body plumage was in some stage of moult. Comparison of moult progress between the sexes is of interest. However, our data on this aspect are limited, and the results include information on unsexed birds handled when captured for ringing.

Of 21 birds checked on 18–26 July, seven (33%) had both old and different stages of new head feathers and the remaining 14 had all head feathers old. In two birds captured on 20 and 23 July, up to 25% of head feathers were growing, with moult scores 1 and 2. Three birds examined on 20, 21 and 23 July and two birds on 25 July had 25% head feathers at a more advanced stage of feather development with moult score 4.

Ten of these birds (two on 22 July, four on 23 July and two on 25 July) had all feathers of the upperparts old without a trace of moult. Singles on 19 July and 20 July had up to 40% and 25%, correspondingly, of growing feathers scored as 1 and 2. Up to 50% of growing feathers with a moult score 3 were recorded on two birds on 19 and 26 July. In the remaining seven birds up to 25% of growing feathers on the upperparts had score 4.

Only three of the 21 birds had not started moult of the underparts (one on 22 July and two on 23 July). Singles on 20, 23 and 25 July had growing feathers with scores 1 and 2, covering up to 25% of the underparts. One captured on 19 July had growing feathers of score 2, covering 25% of the underparts. Growing feathers of score 4, covering 25% of the underparts were found in 11 birds between 18 July and 26 July. Growing feathers of score 4, covering 40–50% of the underparts were recorded in three birds on 19, 20 and 26 July.

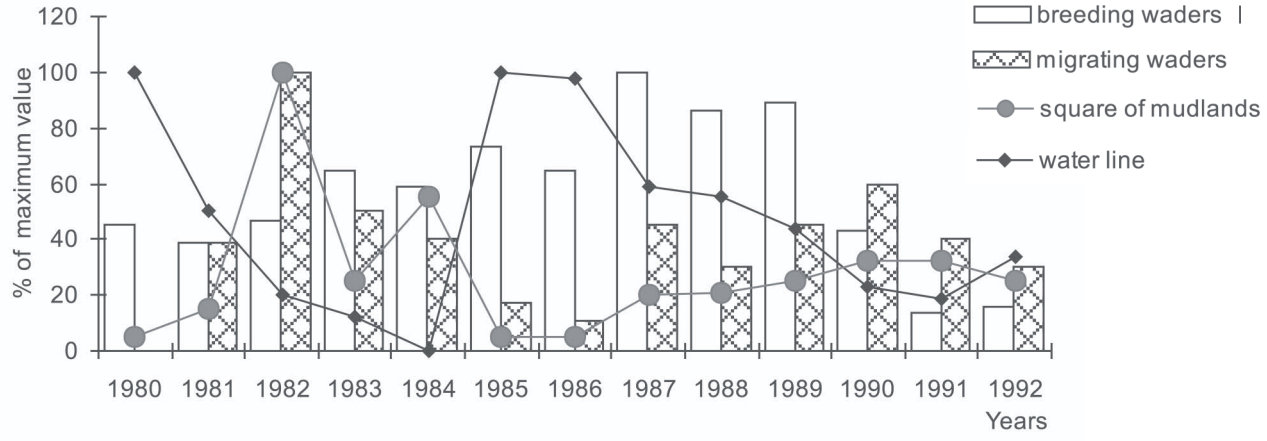

Fig. 3. Variations of shoreline level at Khadyn Lake (Tuva Republic), size of mudflats and dynamics of numbers of migrating (mainly Calidridinae sandpipers) and breeding waders (mainly *Tringa* sandpipers) based on catches (n = 7,521) and transect counts.

Table 7. Numbers of adult and juvenile Curlew Sandpipers in catches at Khadyn Lake, Tuva Republic (by pentades of Berthold): 0 = absence of Curlew Sandpipers in catches; – = no catches were undertaken.

Year	Age	July			August						September				
		40	41	42	43	44	45	46	47	48	49	50	51	52	53
1982	adult	–	–	–	–	–	–	0	1	0	0	0	0	0	0
	juvenile	–	–	–	–	–	–	2	22	32	34	8	14	4	1
1984	adult	24	28	3	0	6	2	4	2	1	0	0	0	–	–
	juvenile	0	0	0	0	0	0	5	31	42	30	38	4	–	–
1987	adult	–	0	0	4	0	1	0	2	0	0	0	0	–	–
	juvenile	–	0	0	0	5	1	0	2	3	1	0	0	–	–
1988	adult	–	–	0	0	0	0	0	0	0	0	0	0	0	0
	juvenile	–	–	0	0	0	2	9	4	2	2	1	1	0	0
1989	adult	–	–	0	0	0	2	0	0	0	0	0	0	0	0
	juvenile	–	–	0	0	0	0	0	0	0	0	0	0	0	0

Six Curlew Sandpipers were examined for moult during the first 10 days of August. All had almost or fully completed the moult of their body feather tracts. One bird on 5 August had new feathers (moult score 5) covering 75% of the head, 25% of the upperparts and 50% of the underparts. Another bird had all its head feathers new, 10% of new feathers on the underparts, and 60% with score 4 and 30% with score 5 on the upperparts. The other four birds had all new head feathers, 40–50% new feathers on the underparts and upperparts.

A sample of males and females sexed on dissection were examined for body moult. One male on 16 July had about 50% of head feathers growing with score 3, 25% with score 1 and 25% with score 2. Four others on 16 July had only old feathers on the head. On 19 July, the head plumage of one male was new. On the upperparts of three males old feathers prevailed (75%) on 16 July. One male examined on 19 July had 60% of old feathers on the upperparts. Growing feathers of score 1 formed 25% on the upperparts of two males on 16 July, and the same proportion of growing feathers of score 4 were found on the upperparts of three males, each one on 16, 17 and 18 July; a male on 19 July had growing feathers of score 4 on 40% of the back. Growing feathers of scores 1 and 2 formed 25% of the underparts of two males on 16 July; three other birds on the same date and two more birds on 17 and 18 August had up to 25% of their underparts growing feathers with scores of 3 and 4. In two males captured on 19 and 22 July, about 40% of growing feathers had score 4.

All head feathers of three females on 17, 18 and 22 July were old; three females examined on 23 July had up to 75% of head feathers old, and 25% of growing feathers with scores 3 (one bird) or 4 (two birds). Five of 10 females examined on 17 and 22 July had 75% of old feathers on the upperparts, with the 25% of growing feathers having score 4. Four other females had 25% of growing feathers with score 3, and one more female had up to 40% of growing feathers on the upperparts with score 4 on 18 July. A female on 17 July had about 50% of the underparts old and the remaining 50% growing feathers of score 4. A female on 18 July had 75% of the underparts at score 4. Five females captured on 22 July, had various stages of feather growth and moult intensity on their underparts. One of them had not started moult of the underparts, one had 25% of growing feathers of scores 1 and 2, and three birds had up to 25% of growing feathers of score 4. A female examined as late as 6 August had growing feathers of scores 3 and 4 covering only 25% of the underparts.

Because adult Curlew Sandpipers displayed a large proportion of feathers in various tracts at different moulting stages, we concluded that they were in active moult of body feather tracts during southward migration. The sequence of moult of the various body tracts followed the pattern described for Curlew Sandpipers by Kozlova (1962). Moult of males started slightly earlier than of females. An arrested moult of body feathers during southward migration was not noted.

Body mass

All birds captured in Ubsu-Nur Depression during northward migration had maximal indices of fat content.

Body masses of males and females of Curlew Sandpipers separated by age and sex, based on museum specimens, are given in Table 9.

Rate of gain of body mass by birds at a stopover site depends on trophic capacity of a wetland, availability of food for birds (Karpova *et al.* 2000), and age of Curlew Sandpipers (Table 10). According to recaptures juvenile birds at Khadyn Lake were increasing their body mass in 1984 with an average rate of 1.2 (SD 0.5) g per day; body mass gain by adults was larger, 4.1 (SD 0.2) g per day (Table 10). Adult birds with fat content evaluated as "much" had mean body mass of 61.3 g, and those with "no" and "little" fat had 47.4 g. The same parameters in juvenile birds were 51.9 g and 41.4 g,

Table 8. Numbers of adult and juvenile Curlew Sandpipers in catches in Trekhozerky Lowland, Khakasia Republic during southward migration (by pentades of Bertoldt). Catching activity in Trekhozerky Lowland took place 17 August–29 October 1990 and 28 July–13 September 1991. ** = this bird was captured at Uskol Lake; 0 = absence of birds in catches; – = no catches were undertaken.

Year	Age	July	August						September				
		42	43	44	45	46	47	48	49	50	51	52	53
1990	adult	–	–	0	0	2	0	0	0	0	0	0	0
	juvenile	–	–	1**	–	30	11	50	64	22	17	0	2
1991	adult	0	8	4	7	2	2	0	0	1	0	–	–
	juvenile	0	0	10	24	66	51	42	40	38	4	–	–

respectively. Of the first-year birds, 79% had "little" or "no" fat content. Based on these figures it would take three to four days for an adult Curlew Sandpiper and eight to nine days for a first-year bird to gain the body mass upper limit.

Mean body mass of adults caught for ringing was 55.0 g (SD 1.07 g, n = 50), significantly larger ($P < 0.01$) than in first-year birds, 45.7 g (SD 0.98 g, n = 50). The mean wing length of adults, 134.5 mm (SD 0.73 mm, n = 50) was not significantly different from that of juveniles, 133.2 mm (SD 0.32 mm, n = 55). Thus the difference in body mass between adults and juveniles was apparently related to the amount of accumulated fat. This was confirmed by proportions of Curlew Sandpipers with large fat score during southward migration in 1984: it was 56% in adults and 7% in first-year birds. Comparison of body masses of Curlew Sandpipers by pentades during the whole period of southward migration revealed a consistent age difference in body mass (Fig. 4).

Table 9. Body mass (g) of Curlew Sandpipers obtained from specimens collected on southward migration at Khadyn Lake, Tuva Republic: M male; F female; U unsexed.

Year	Sex, age	*n*	Range	Mean	SD	*P*
1982	U, juv	100	41.0–63.5	49.7	4.8	–
1984	F, ad	10	49.7–68.0	57.8	6.9	n.s.
	M, ad	11	50.5–63.4	55.7	3.7	
	F, juv	1		40.8	–	–
	M, juv	4	36.2–52.4	42.9	7.2	–
1987	U, ad	4	44.6–70.1	61.5	11.8	n.s.
	U, juv	8	46.5–62.7	51.2	6.8	

Duration of stay at stopover sites

No data are available about duration of stopovers on northward migration by Curlew Sandpipers in southern Central Siberia, but it is likely to be short. Southward migration lasts more than two months, and recaptures of ringed birds indicate that individual Curlew Sandpipers stay at a site in July–September for as long as 14–16 days with median durations between two and five days on different wetlands (Tables 11–13). Based on large samples obtained at Bele Lake and Trekhozerky Lowland the mean stopover duration of adults was 5.3 days and of juveniles was 3.8 days. First-year birds had smaller rates of body mass gain than adults; in spite of this their average stopover time at a wetland was shorter than adults.

Ring recoveries and migratory directions

Three distant recoveries of Curlew Sandpipers document transcontinental links of birds on southward passage across the southern Central Siberia. Two juvenile Curlew Sandpipers, one ringed on 26 August 1990 (Moskwa XD034615) at Trekhozerky Lowland, Khakasia Republic, and another ringed on 28 August 1982 (Moskwa 553319) at Khadyn Lake, Tuva Republic, were recaptured on 6 October 1993 at Werribee Sewage Farm, Melbourne, south-eastern Australia (38°05'S, 144°31') and on 3 October 1983 at 80 Mile Beach, north-western Australia (19°15'S, 121°25'E), respectively. An adult Curlew Sandpiper (Canberra 041-14089) ringed at Port Headland Saltworks (20°11'S, 118°54'E) was recaptured at Bele Lake, Khakasia Republic, on 18 August 1985 (Minton 1998, 2002).

The intensity and direction of southward migration by Curlew Sandpipers at Khadyn Lake, Central-Tuva Depression, in 1982, and at Tryokhozerki Lowland, Southern-Minusinsk Depression, in 1990 and 1991, based on visual observations showed a south-eastward direction (Fig. 5). Thus, the direction of the visual observations coincided with that of the ring recoveries.

DISCUSSION

Historical status

At the beginning and middle of the 20th century migration of Curlew Sandpiper in southern Central Siberia was recorded irregularly. Tugarinov & Buturlin (1911) wrote that birds were found in flocks up to 40 individuals in Krasnoyarsk District in July and August. They also stated that some birds remained in the region during the breeding season. Tugarinov (1927) mentioned Curlew Sandpiper as a migratory species in his list of birds of Central Siberia (region along the Yenisey River).

Curlew Sandpipers were observed by Sushkin (1914) in small numbers in Minusinsk Depression as a roving and migratory bird of steppe lakes. In Tuva Republic he recorded Curlew Sandpiper at Khadyn and Chagytay Lakes in rather large numbers in early August. Flocks up to 50 individuals, were found "at salty wet shores of small lakes surrounding Khadyn Lake". However, later Yanushevich (1952) did not include Curlew Sandpiper on the list of birds of Tuva Republic, thus probably indicating an absence of the species from

Table 10. Rate of body mass gain by Curlew Sandpipers based on recaptures at Khadyn Lake, Tuva Republic, in 1984.

Ring number	Age	Date first captured	Body mass at first capture (g)	No. of days between captures	Difference in body mass between captures (g)	Main daily gain in body mass (g/day)
P728209	adult	16 July	44.9	5	+20.0	+4.0
P728247	adult	24 July	42.8	5	+20.1	+4.02
P728222	adult	21 July	57.0	1	+4.2	+4.2
P728260	juvenile	18 August	46.8	5	+3.1	+0.62
P729751	juvenile	1 September	42.2	4	+8.3	+2.08
P729711	juvenile	26 August	42.5	3	+1.7	+0.57
P728263	juvenile	21 August	45.0	3	+3.0	+1.0
P729772	juvenile	4 September	46.5	3	+4.2	+1.4
P729755	juvenile	3 September	42.3	2	+2.7	+1.35
P729772	juvenile	4 September	46.5	2	+2.7	+1.35

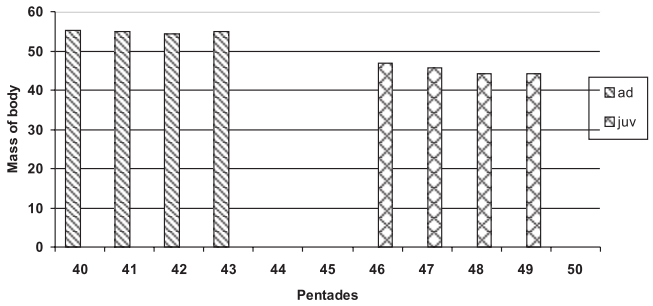

Fig. 4. Body mass of Curlew Sandpipers at Khadyn Lake, Tuva Republic, based on inspection of live birds in 1984.

Table 11. Intervals between capture-recaptures of the same Curlew Sandpipers at Khadyn Lake, Tuva Republic, in 1984.

Dates of captures of the same birds	No. of days between captures	No. of captured birds
16–17 and 21–22 July	1	2
24–26 July, 3–5 and 4–6 Sept.	2	3
21–24 Aug., 4–7 Sept.	3	2
1–5 Sept.	4	1
18–23 Aug., 1–6 Sept.	5	2

the region in mid 1940s, the years of his survey.

More recently Curlew Sandpiper has become a regular migrant in southern Central Siberia. However, as shown in this study, numbers of the species varied between years. As in most European regions, irruptions of this species occur (Glutz *et al.* 1975). Records of Curlew Sandpiper in subtaiga and south taiga subzones are infrequent; we had no records in taiga along the rivers of the region between Ob' and Yenisey Rivers (Savchenko *et al.* 2001a,b). This wader was not included on the list of bird species of subtaiga subzone of Western Siberia (Yudkin 2002); however, Strelkov (1973) observed flocks of 200–300 Curlew Sandpipers each on 24 May 1972 at Narym River, a tributary of the middle Ob' River.

On wetlands in steppe and forest-steppe Curlew Sandpipers were found throughout the region. In some sites and years it was recorded in large numbers in areas such as the basin of the Angara River, Bratsk Reservoir and Baikal Lake (Tolchin *et al.* 1977). It was common in the delta of Selenga River (Shvetsov & Shvetsova 1967, Fefelov *et al.* 2001) and in Mongolia (Ostapenko *et al.* 1980, Fomin & Bold 1991). All these data indicate that Curlew Sandpiper migrates in a wide front in southern Siberia.

Northward migration

Curlew Sandpipers usually leave their non-breeding grounds in April (Gladkov 1951, Glutz *et al.* 1975). The northward migration across southern Central Siberia is brief and is less conspicuous than the southward one. There are

Table 12. Intervals between capture and recapture of the same Curlew Sandpipers at Bele Lake, Khakasia Republic, in August 1985.

Dates of captures of the same birds	No. of days between captures	No. of captured birds
10–11; 12–13; 12–13; 16–17; 16–17; 16–17; 16–17; 17–18; 18–19; 20–21; 21–22	1	11
9–11; 11–13; 11–13; 12–14; 14–16; 17–19; 17–19; 18–20; 19–21; 19–21; 19–21; 20–22; 20–22	2	13
12–15; 17–20; 17–20; 18–21; 17–20; 19–22	3	6
11–15; 12–16; 14–18; 18–22; 20–24	4	5
10–15; 11–16; 11–16; 14–19; 14–19; 17–22	5	6
11–17; 11–17; 11–17; 16–22	6	4
17–24; 17–24	7	2
8–16; 11–19; 16–24	8	3
14–24; 14–24	10	2
1–12	11	1
10–24	14	1

Table 13. Intervals between capture-recaptures of the same Curlew Sandpipers in Trekhozerky Lowland, Khakasia Republic, in 1990 and 1991.

Dates of captures of the same birds	No. of days between captures	No. of captured birds
1990: 27–28 August; 30–31 August; 31 August–1 September; 31 August–1 September	1	4
1991: 11–12 August; 24–25 August; 24–25 August	1	3
1990: 27–29 August; 28–30 August; 31 August–2 September	2	3
1991: 18–20 August; 20–22 August; 20–22 August; 23–25 August; 8–10 September	2	5
1990: 29 August–1 September	3	1
1991: 5–8 September	3	1
1990: 28 August–1 September; 2–6 September	4	2
1991: 9–13 August; 14–18 August; 16–20 August	4	3
1990: 27 August–1 September; 27 August–1 September; 28 August–2 September	5	3
1991: 8 August–14 August; 14–20 August; 3–9 September	6	3
1990: 11–18 September	7	1
1990: 11–19 September	8	1
1990: 1–10 September	9	1
1991: 12–22 August	10	1
1991: 18–29 August; 30 August–10 September	11	2
1990: 12–28 September	16	1

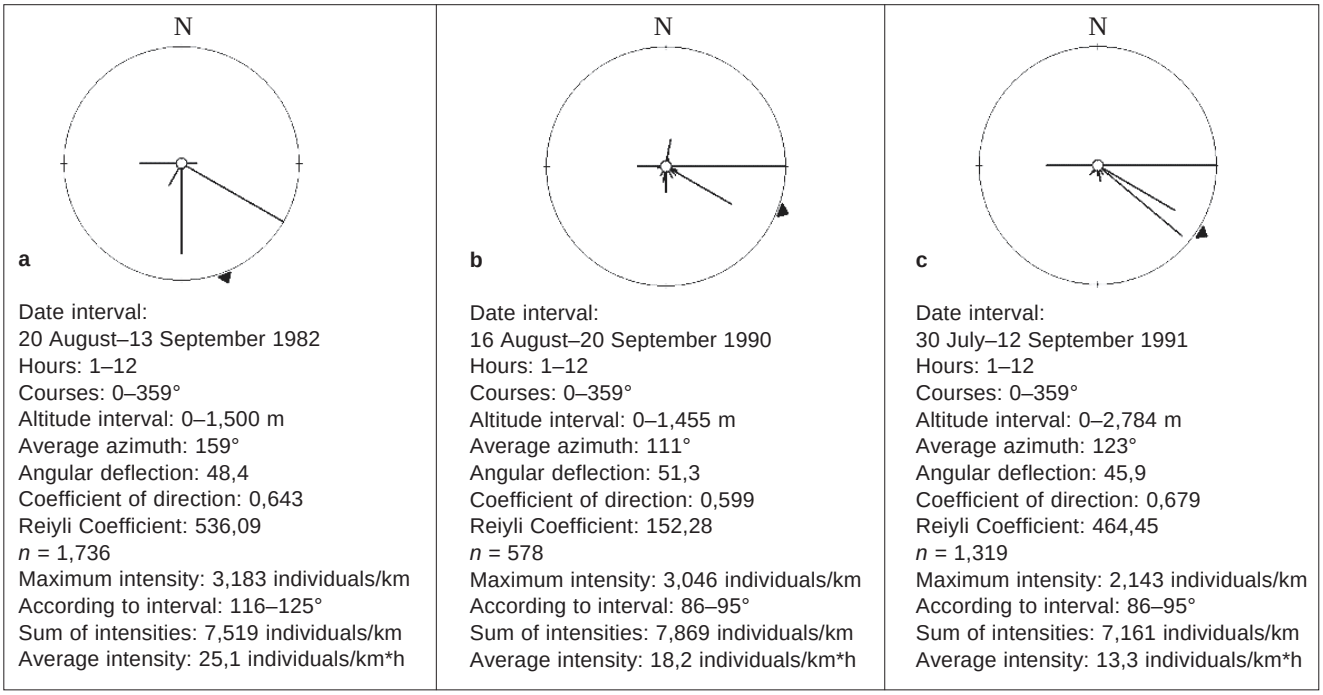

Fig. 5. Intensity and direction of southward migrations of Curlew Sandpipers: **a** – at Khadyn Lake, Central-Tuva Depression, in 1982; **b** – at Tryokhozerki Lowland, Southern-Minusinsk Depression, in 1990; **c** – at Tryokhozerki Lowland, Southern-Minusinsk Depression in 1991, based on visual-optical observations. Line – direction or vector of migration; length of line in every 10° sector corresponds to intensity of migration; triangle – average azimuth.

far fewer sites at which this species has been recorded on northward migration to breeding grounds than on southward migration. In general, records of Curlew Sandpipers in southern Central Siberia during northward migration are not numerous. Based on the available data, we conclude that a difference of five to seven days exists in the start of the migration between in Ubsu-Nur and Central-Tuva Depressions and also that birds appear in Central-Tuva and Minusinsk Depressions simultaneously. Passage of Curlew Sandpipers at the latitude of Krasnoyarsk is most often in early June, as in Minusinsk Depression. Birds make brief stops in southern Central Siberia at slightly different times in Ubsu-Nur and Minusinsk Depressions.

Curlew Sandpipers captured in Ubsu-Nur Depression on northward migration had maximal fat scores and were ready for a long passage. Peak northward migration of Curlew Sandpipers across southern Central Siberia coincides with a period of deterioration of feeding conditions due to a sharp raise of water levels in rivers and lakes during the thaw. The near complete absence of records of the species in the northern part of the region probably indicates a non-stop passage of birds across a wide forested area, the taiga zone. Such long distance flights are characteristic of Curlew Sandpipers (Johnson 1974, Glutz *et al.* 1975); however, this is not a sufficient explanation for the absence of Curlew Sandpipers from several favourable sites. For example, there was a rather intensive migration of other species of sandpipers (Temminck's Stint *Calidris temminckii*, Long-toed Stint *C. subminuta*, Dunlin *C. alpina*) at Khadyn Lake in late May 1983, but only a few Curlew Sandpipers were present. If birds arrive on the western portions of their breeding grounds in the first half of June (Glutz *et al.* 1975, Danilov *et al.* 1984, Yestafyev *et al.* 1995, Tomkovich & Soloviev 2006) then the main sites of their brief stopovers in southern Central Siberia are likely to be wetlands of depressions in the region of Altai and Sayany Mountains.

Southward migration

Records of Curlew Sandpipers during the period between northward and southward migrations (from the second week of June till mid July) are rare in southern Central Siberia. Southward migration starts with the arrival of adult males in the second 10-day period of July. They leave breeding grounds while females are incubating (Glutz *et al.* 1975); this occurs on the Taimyr Peninsula in the first third of July. Unsuccessful females follow males, but females which breed successfully start migration mostly in late July; farther east, in Yakutia, these events take place slightly earlier (Tomkovich & Soloviev 2006). Adult males arrive at and depart from Australian nonbreeding grounds on average earlier than adult females (Barter 1987). Arrival of females in southern Central Siberia as early as July 1984 is apparently a result of unsuccessful nesting in that year, same phenomenon was noted for the Baikal region as well (Summers & Underhill 1987, Fefelov *et al.* 2001).

First-year birds appeared on wetlands of southern Central Siberia in the second five-day period of August. In some years they have peak passage in the last third of August and in early September; this probably takes place in years of good breeding productivity. The delayed migration schedule of juvenile in relation to adult Curlew Sandpipers continues onto their arrival to non-breeding grounds. Thus, adults arrive in Australia in late August and early September, juvenile birds arrive four to six weeks later (Barter 1987).

A loop migration is known for a number of North American waders (McNeil & Cadieux 1972) and may occur with Curlew Sandpiper. Possibly some Curlew Sandpipers return to their non-breeding grounds using different routes from those used for their northward passage, and some juveniles possibly use this route for only their first southward migration to Australia (Minton 1998).

Directions of migrations and migratory links

No data exist for breeding origin of Curlew Sandpipers on passage across southern Central Siberia. However, based on ring recoveries the migratory links with Australian non-breeding grounds are now certain. These links are unexpected because a south-westward direction of post-breeding migration prevails on the Yenisey Plain and central parts of Krasnoyarsk Region (Savchenko *et al.* 2001b); Kozlova (1962) suggested that Curlew Sandpipers from Yenisey River migrate to nonbreeding grounds in India and Sri Lanka.

It is also known that a juvenile Curlew Sandpiper ringed on its first migration on 26 August 1976 at Chany Lake, Western Siberia, was captured in southern India on 8 August 1980, and a Curlew Sandpiper ringed in south-eastern Australia in January 1988 was recaptured as a territorial male on the Taimyr Peninsula in late June 1991 (Minton 2002). One more observation exists for Taimyr Peninsula of an Australian Curlew Sandpiper with a colour mark, but also many other recoveries are known there from India, Africa and Europe, with the latter being the most common. All these recoveries indicate that either a conventional divide between western and eastern flyways of the species that lead to Indian and Australian non-breeding grounds, respectively, is situated in the area of the upper Ob' and Yenisey Rivers, or that the flyways leading birds to various non-breeding grounds overlap there.

Spacing and numbers

In spite of the wide front of migration of Curlew Sandpipers, the irregular spatial distribution corresponds with the irregular location of wetlands having ecological conditions favourable for the species. Because the study region is characterized by a continental arid climate, formation of extensive mudflats on naturally closed water bodies is an uncommon phenomenon because the water table drops sharply during the summer season. The gradual decrease of the water table in hot months and a strong insolation cause formation of salt marshes, dry sandy beaches and a hard layer ("crust") on clay deposits, none of which are suitable feeding habitats for Curlew Sandpipers.

Kozlova (1962), Leonovich (1973) and others pointed to specific methods of feeding of Calidridinae sandpipers, related to their morphological features. Open mudflats of salty or brackish lakes, less often silted gravel or pebble shores of fresh water bodies, are the best habitats of Curlew Sandpipers. These sandpipers occur rarely on typical lakes of taiga, on rivers with banks of tussocky sedges or built up of clear pebble, gravel or rocks. Curlew Sandpipers also avoid sandy beaches in steppe and desert landscapes. Importance of subtle differences in substratum on feeding of sandpipers was shown by Quammen (1982). We believe that the restricted number of wetlands with the suitable feeding conditions in continental part of Asia results in a rapid appearance of concentrations of Curlew Sandpipers when suitable wetlands come into existence. Surveys of the region have shown that the range of habitats with favourable ecological conditions for sandpipers have been extended recently due to the construction of artificial water bodies of anthropogenic origin. Nevertheless, sites with large concentration of Curlew Sandpipers in the region are not numerous.

The fast response of birds to the appearance of suitable feeding sites confirms indirectly that the number of passing Curlew Sandpipers is much higher than can be traced from counts in sites of bird staging during migrations. We compared the data available for Tuva and Khakasia with observations in other continental parts of Asia: Kazakhstan (Dolgushin 1962, Gavrin 1973, Gavrilov & Gavrilov 1978, Yerokhov 1978), Western Siberia (Yurlov 1975, Dubovik *et al.* 1977, Moskvitin *et al.* 1980, Vengerov 1980, Yurlov 1981, Moskvitin *et al.* 1983), Baikal Lake and Transbaikalia (Tolchin *et al.* 1973, Tolchin 1975, Tolchin *et al.* 1977, Pyzhyanov & Popov 1978, Fefelov *et al.* 2001). Our conclusion is that a substantial part of Siberian Calidridinae sandpipers, Curlew Sandpipers in particular, migrate across southern Central Siberia. Taking into account numbers of key staging sites and intensity of passage in areas of main migration, we assess that the numbers of Curlew Sandpipers on southward migration in years of successful breeding can be estimated as being at least 35,000–40,000 birds in southern Central Siberia.

Patterns of migration

Juvenile Curlew Sandpipers stage at stopover sites on average for 1.4 days shorter than adults and at the same time they accumulate body mass 3.4 times more slowly; this suggests that juveniles undertake a large number of short-distance migrations and helps explain the different patterns of migration between the adults and juveniles. Clearly, adults migrate with fewer stops and longer journeys to key areas of their flyway than do juveniles. Rather short-distance movements from one wetland to another must prevail among juveniles during their first migration across southern Central Siberia. This probably explains not only the prolonged period of presence of juveniles in the region, but also their occurrence on a much larger number of wetlands of various types as well as their numerical predominance in catches.

In contrast to adult birds, which are able to combine migration with body moult and at the same time to restore their energy reserves rapidly on stopovers, juveniles have more extended migration (also recorded by Wilson *et al.* 1980, Gromadzka 1985) and this is probably related not only to physiological but also to behavioral characteristics. It cannot be excluded that the biological importance of short-distance movements to juvenile Curlew Sandpipers is primarily a necessity to form links with geographic areas for future migrations. This phenomenon is also related to distant dispersion.

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