

# Timing of migration of the Curlew Sandpiper (*Calidris ferruginea*) through Poland in relation to Arctic breeding conditions

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Recent shifts in the timing of migration and breeding have been attributed to climate variation in some migratory birds. However, the divergent patterns in the timing of autumn migration among different bird species suggest a significant role of factors other than climate. Using data of constant-effort catches, determinants for the annual variation in the timing of migration were investigated in the Curlew Sandpiper *Calidris ferruginea* in Poland. Variation in the timing for adult and juvenile Curlew Sandpipers was influenced by breeding success, which was in turn connected to predation pressure, and June and July temperatures on the species' breeding grounds in the Arctic region. Median date of passage of adults was significantly later in good than in poor breeding years. The migration of adults was earlier by 2.3 days for every 1°C increase in average June temperature in the Arctic breeding grounds. Median migration date of juveniles was positively correlated with predation and negatively with June temperature in the Arctic breeding grounds. Median migration date of adults advanced by a factor of  $-0.59$  days/year, which translates into 10 days from 1984–2000. These results suggest that conditions on breeding grounds can affect the timing of subsequent events within the annual cycle. Circumstantial evidence also suggests that climate change may have increased the predation on young Curlew Sandpipers, increasing the frequency of poor breeding years and modifying the timing of autumn migration in these waders.



## 1. Introduction

In many migratory Arctic breeding waders, autumn (post-breeding) migration begins as soon as parental responsibilities are completed (Tomkovich & Soloviev 2006, Meltotte *et al.* 2007). Factors which affect the onset and duration of the breeding season can therefore influence the timing

of autumn migration. Weather conditions in the Arctic region prior to and during the breeding season can directly or indirectly influence the starting dates of breeding and ultimately the breeding success (Schekkerman *et al.* 1998, Tomkovich & Soloviev 2001, Beal *et al.* 2006). For instance, the onset of egg-laying can be delayed when the ground is still covered by snow when birds arrive

to the breeding grounds (Summers & Underhill 1996, Møltøfte *et al.* 2007), low temperatures can reduce the abundance of insects and thereby delay the initiation of egg-laying (Møltøfte *et al.* 2006), and wind chill can interfere with mating and incubation (Tomkovich 1995).

In species such as the Curlew Sandpiper *Calidris ferruginea* and the Red Knot *C. canutus*, the timing and intensity (i.e., number of individuals passing through per day) of autumn migration is influenced by the level of predation on their eggs and chicks (Blomqvist *et al.* 2002, Meissner 2005, Figuerola 2006, Tomkovich & Soloviev 2006). Predators such as the Arctic Fox *Alopex lagopus* switch from a diet of lemmings, *Lemmus* spp. and *Dicrostonyx* spp., to the eggs and young of Arctic breeding birds following a year of decreasing lemming abundance (Underhill 1987, Summers *et al.* 1998, Bęty *et al.* 2001), thereby prematurely ending the birds' breeding season. Consequently, the timing of migration in these species appears correlated with lemming abundance and predation pressure in the Arctic region (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006).

Current knowledge on bird migration indicates that spring arrival dates for many species breeding in the northern hemisphere have advanced during the second half of the 20<sup>th</sup> century in response to warming climate (Gordo 2007, Rubolini *et al.* 2007). Changes in the timing of autumn migration, however, are more variable, and the observations cannot be explained simply by climatic variation. For instance, there is an advancement of autumn migration in some long-distance migrants and a delay in short-distance migrants (Jenni & Kéry 2003). Species which lay a single clutch have advanced their autumn migration, while species with a double-clutch system have delayed their migration (Jenni & Kéry 2003). Autumn migration dates of the Greenshank *Tringa nebularia*, Spotted Redshank *T. erythropus* and Wood Sandpiper *T. glareola* have advanced (Anthes 2004), while that of Ruff *Philomachus pugnax* has delayed (Adamik & Pietruszková 2008), presumably in response to climate change.

Some studies have considered the role which climate change plays in altering trophic-level interactions, eventually leading to a change in the

demography and life-history traits of the interacting organisms (Harrington *et al.* 1999, Ims & Fuglei 2005). Other studies have demonstrated that climate change has declined the regularity of lemming peaks (Hörnfeldt *et al.* 2005, Kausrud *et al.* 2008). These studies predict that the scarcity of lemmings will push predators such as foxes to increasingly often prey on other species, including waders. Assuming that predation on the eggs and young of Arctic waders has increased, the timing of autumn migration in the Curlew Sandpiper may have become earlier over the recent decades. This predicted relationship between the timing of migration and the changing biotic and abiotic conditions on the breeding ground is explored in the present study.

Waders (shorebirds) migrating along the East Atlantic Flyway often use the southern coast of the Baltic Sea, near Gdańsk, Poland, as a stop-over site (Gromadzka 1987). One of the more numerous species caught there is the Curlew Sandpiper (Meissner *et al.* 2009). This species breeds in the Arctic tundra north of 65°N in central Siberia, and over-winters in Africa, southern Asia and Australasia. Curlew Sandpipers reach their breeding area in June (Syroechkovski & Lappo 1994) and egg-laying starts between 15–22 June (Tomkovich & Soloviev 2006). Only females incubate and most males leave their territories soon after the females begin incubating. Autumn migration of males starts by early July while the females migrate after the young have fledged or when breeding fails (Holmes & Pitelka 1964, Tomkovich 1988).

Until now, a thorough examination of the relationship between the timing of migration, reproductive success and conditions at breeding areas in waders breeding in the Arctic region has been lacking. Many studies routinely attribute changes in migration phenology to climate, but few have examined the complex relationship between events in the annual cycle. The aim of the present study, therefore, was to examine the migratory pattern of adult and juvenile Curlew Sandpipers through Poland with respect to breeding conditions in the Arctic breeding grounds, and to quantify the trend in the timing of migration in the period 1984–2000 in relation to variation in temperature and predation.

## 2. Material and methods

The study topic was examined using ringing and count data collected during 1983–2000 by the Polish Waterbird Research Group KULING. Birds were caught using walk-in traps on the Puck Bay coast at three sites on the inner coast of the Gulf of Gdańsk, Poland: Jastarnia (54°42' N, 18°40' E), Rewa (54°37' N, 18°39' E), and at the Reda River mouth (54°37' N, 18°47' E; Fig. 1). Birds were aged according to Prater *et al.* (1977). Wing length (maximum chord; Evans 1986), bill length (Prater *et al.* 1977), and weight were measured. Measurement of wing length was taken to the nearest 1 mm and weight to the nearest 1 g. The ability and consistency of ringers in measuring were checked annually according to Busse (1994). In addition to ringing, three counts were conducted daily at Jastarnia and Rewa, while waders were counted only once a day at about midday at Reda (Meissner *et al.* 2009). At Jastarnia and Rewa – where three counts per day were conducted – maximum numbers were taken into account.

To correct for differences in sample size at the three sites, the number of birds counted per day was converted into a proportion of the total number of birds recorded that year. From the ringing data, adult birds were separated into sex classes using the discriminant function equation developed by Wymenga *et al.* (1990). The discriminant score (D) was computed as

$$D = 0.07815 * W + 0.47962 * B - 28.7302 \quad (1)$$

where W = wing length (mm) and B = bill length (mm). For males,  $D < 0$  and for females,  $D > 0$ . As the proportion of birds in count data is comparable to that in ringing data (Meissner 2006), migration patterns for males and females obtained from ringing data accurately reflect the overall pattern of migration. The timing of field work differed between years, and the analyses were therefore restricted to the period between 19 July and 27 September (data available for every year).

The timing of autumn migration was examined in relation to breeding success and conditions in the Arctic breeding ground. Using count data, annual median migration dates (the date at which 50% of passage had taken place) were computed separately for adults and juveniles. Using ringing

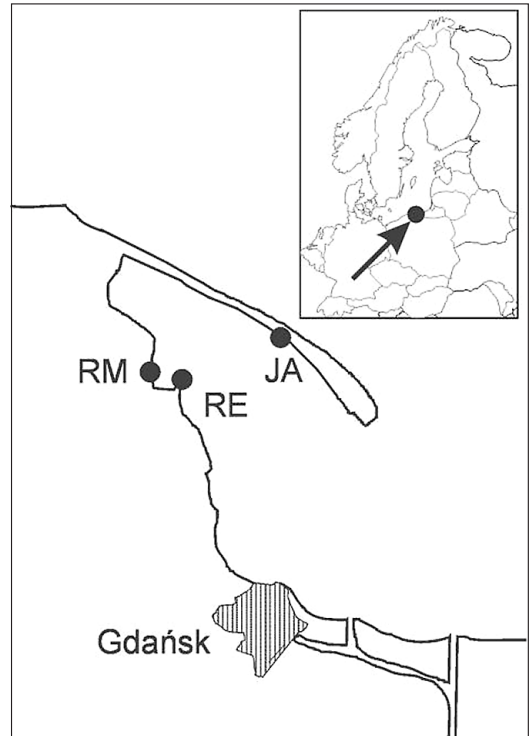


Fig. 1. Study area at the Baltic Sea coast, northern Poland. RM = Reda mouth; JA = Jastarnia; RE = Rewa. Adapted from Meissner (2006).

data, yearly median migration dates were computed for adult males and females. Median (rather than mean) dates were used because these data were not normally distributed. General linear models (GLM) were used to compare migration dates in good and poor breeding years, examining the effects of temperature and predation on the timing of migration of adults and juveniles, and on adult males and females.

The median migration date of each year was the dependent variable, sex and breeding success were fixed factors, and the average monthly temperatures in June and in July, and a predation index, were included in the model as covariates. The predation index was obtained from Blomqvist *et al.* (2002), where predation represents an assessment of the likelihood that wader nests and chicks will be depredated based on the abundance of lemmings. This index ranges from 0 (low predation pressure) to 3 (high predation pressure). Two-way interactions of the above-listed terms were also modelled.

Table 1. Annual total counts and lower percentiles (P25), medians and upper percentiles (P75) for migration dates of adult and juvenile Curlew Sandpipers passing through Poland (1984–2000).

Year	Adults		Migration dates, adults			Juveniles		Migration dates, juveniles		
	n	%	P25	Median	P75	n	%	P25	Median	P75
1984	709	0.63	30 Jul	11 Aug	24 Aug	421	0.37	25 Aug	4 Sep	14 Sep
1985	637	0.27	27 Jul	7 Aug	20 Aug	1,743	0.73	29 Aug	7 Sep	16 Sep
1986	460	0.42	27 Jul	11 Aug	24 Aug	629	0.58	26 Aug	5 Sep	16 Sep
1987	710	0.89	28 Jul	5 Aug	14 Aug	86	0.11	19 Aug	28 Aug	03 Sep
1988	710	0.89	28 Jul	5 Aug	14 Aug	86	0.11	19 Aug	28 Aug	03 Sep
1989	180	0.82	25 Jul	4 Aug	10 Aug	39	0.18	19 Aug	3 Sep	20 Sep
1990	514	0.68	22 Jul	30 Jul	18 Aug	245	0.32	24 Aug	29 Aug	05 Sep
1991	109	0.49	19 Jul	29 Jul	23 Aug	112	0.51	25 Aug	2 Sep	09 Sep
1992	170	0.73	23 Jul	29 Jul	03 Aug	64	0.27	30 Aug	11 Sep	16 Sep
1993	546	0.55	24 Jul	6 Aug	18 Aug	442	0.45	21 Aug	30 Aug	16 Sep
1994	260	0.70	19 Jul	24 Jul	22 Aug	113	0.30	24 Aug	28 Aug	04 Sep
1995	524	0.87	21 Jul	26 Jul	13 Aug	77	0.13	16 Aug	21 Aug	05 Sep
1996	533	0.60	23 Jul	5 Aug	24 Aug	352	0.40	31 Aug	9 Sep	19 Sep
1997	405	0.38	20 Jul	30 Jul	14 Aug	670	0.62	21 Aug	30 Aug	07 Sep
1998	689	0.73	20 Jul	2 Aug	17 Aug	253	0.27	24 Aug	5 Sep	14 Sep
1999	400	0.38	19 Jul	1 Aug	12 Aug	658	0.62	26 Aug	6 Sep	17 Sep
2000	321	0.72	21 Jul	31 Jul	10 Aug	126	0.28	21 Aug	6 Sep	19 Sep

Trends in median migration dates during 1983–2000 for adults and juveniles were also examined using GLM. The annual median migration date was the dependent variable, and the predation index and average June temperature were continuous variables. The model also included second-order interactions of these variables. The slope (*b*) provided a measure for the magnitude and direction of the trend.

The proportion of juveniles from the total number of observed birds was used as a measure of breeding success (Melfoite 2001, Minton *et al.* 2005). Because breeding success in the Curlew Sandpiper usually exhibits a “boom-or-bust” pattern (Summers *et al.* 1998), years with the proportion of juveniles more than 0.20 were classified as “good”, and years when juveniles were less than 0.20 were classified as “poor” (Summers & Underhill 1987, Schekkerman *et al.* 1998); intermediate years were excluded from the analysis.

Data on average June and July temperatures were used as a proxy for weather conditions in the Arctic region during the breeding period (Tomkovich & Soloviev 2006). Daily temperature data from two weather stations located in the Taimyr Peninsula (77°23'N) were obtained from the website of the National Oceanic and Atmo-

spheric Administration (NOAA). Averages of June and July temperatures were calculated from the two weather stations. Statistica 9 (Stasoft 2010) was used for all analyses.

### 3. Results

The number of birds recorded among the three sites differed but the the proportion of birds caught per day was similar (Kolmogorov-Smirnov test:  $D = 1.10$ ,  $P = 0.58$ ); therefore, data from the three sites were combined for further analysis. In total, 15,344 birds (6,938 adults and 8,406 juveniles) were counted between 1984 and 2000. Additionally, 1,077 adults and 1,054 juveniles were caught and measured during 1983–2000. The annual numbers of adults varied between 109 in 1991 and 709 in 1984, and juveniles varied between 39 in 1989 and 1,743 in 1985 (Table 1). After controlling for variation in observation effort among the three sites, there was no significant trend in the number of adults observed on migration during the period of 1983–2000 ( $F_{1,701} = 1.279$ ,  $P = 0.132$ ,  $b = -0.186$ ), but there was a significant decline in the number of juveniles ( $F_{1,534} = 14.450$ ,  $P < 0.001$ ,  $b = -0.644$ ).

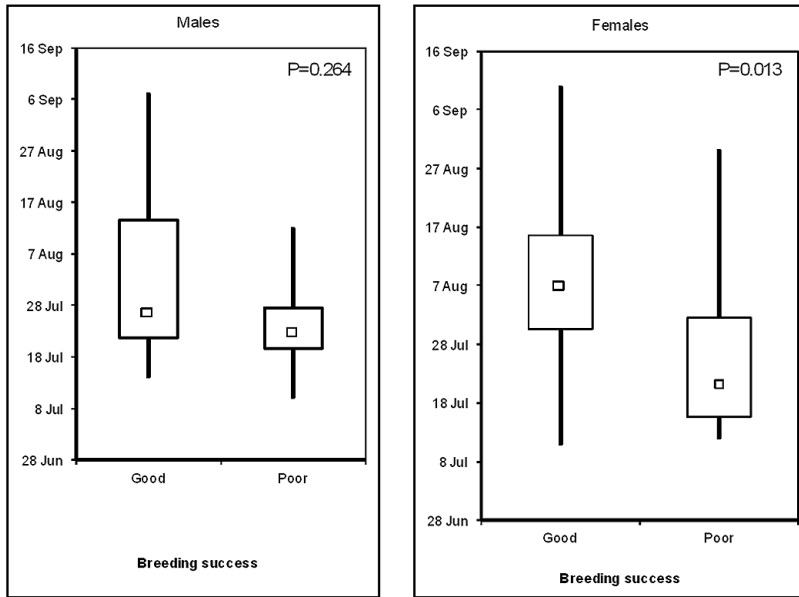


Fig. 2. Median migration dates of the passage of adult male and female Curlew Sandpipers in good and poor breeding years through Poland. Estimates are from ringed birds (1983–2000).

### 3.1. Autumn migration of adults

The median migration date of adults in good breeding years (see Material and methods) was 4 August, eight days later than the median migration date in poor breeding years on 27 July ( $F_{1,632} = 6.80, P = 0.026$ ). Birds migrated about 2.6 days earlier for every unit increase in the index of predation ( $F_{1,632} = 7.62, P = 0.010, b = -2.57$ ). Also, birds migrated 2.3 days earlier for every  $1^{\circ}\text{C}$  raise in average June temperature ( $F_{1,632} = 10.32, P = 0.014, b = -2.32$ ). There was no significant effect of the average July temperature on the timing of migration in adults ( $F_{1,632} = 0.30, P = 0.594, b = -1.10$ ). The interaction between breeding success and the predation index was significant ( $F_{1,632} = 5.91, P = 0.035, b = -6.29$ ), indicating that as predation pressure increased, the difference between the timing of migration in good and poor breeding years became more pronounced.

### 3.2. Autumn migration of juveniles

Median migration date of juveniles in good breeding years was 29 August, seven days earlier than the median migration date in poor breeding years (5 September). This difference between good and poor years was not statistically significant, how-

ever ( $F_{1,523} = 0.41, P = 0.525$ ). Median migration date of juveniles was significantly affected by the average June temperature ( $F_{1,523} = 12.99, P = 0.003, b = -2.85$ ) and the predation index ( $F_{1,523} = 4.29, P = 0.038, b = 1.91$ ) but not by July temperature ( $F_{1,523} = 1.89, P = 0.168, b = -0.48$ ).

### 3.3. Sex differences in migration phenology

Median migration date of males was 23 July, which was significantly earlier than that of females (4 August;  $F_{1,998} = 8.81, P = 0.003, b = -7.94$ ). For males, median migration date was 28 July in good and 23 July in poor years ( $F_{1,607} = 1.48, P = 0.264$ ; Fig. 2). For females, median migration date was 6 August in good years, which was significantly later than that in poor years (23 July;  $F_{1,468} = 7.10, P = 0.013$ ; Fig. 2).

In males, migration dates were significantly affected by June temperature ( $F_{1,607} = 3.85, P = 0.041, b = -1.01$ ) but not by July temperature ( $F_{1,607} = 0.31, P = 0.586, b = -0.91$ ) or predation index ( $F_{1,607} = 0.78, P = 0.784, b = 0.54$ ). In contrast, the migration dates of females were significantly related to the predation index ( $F_{1,468} = 5.341, P = 0.021, b = -2.65$ ) and July temperature ( $F_{1,468} = 19.08, P < 0.001, b = 1.69$ ) but not with June temperature ( $F_{1,468} = 0.19, P = 0.672, b = 0.79$ ).

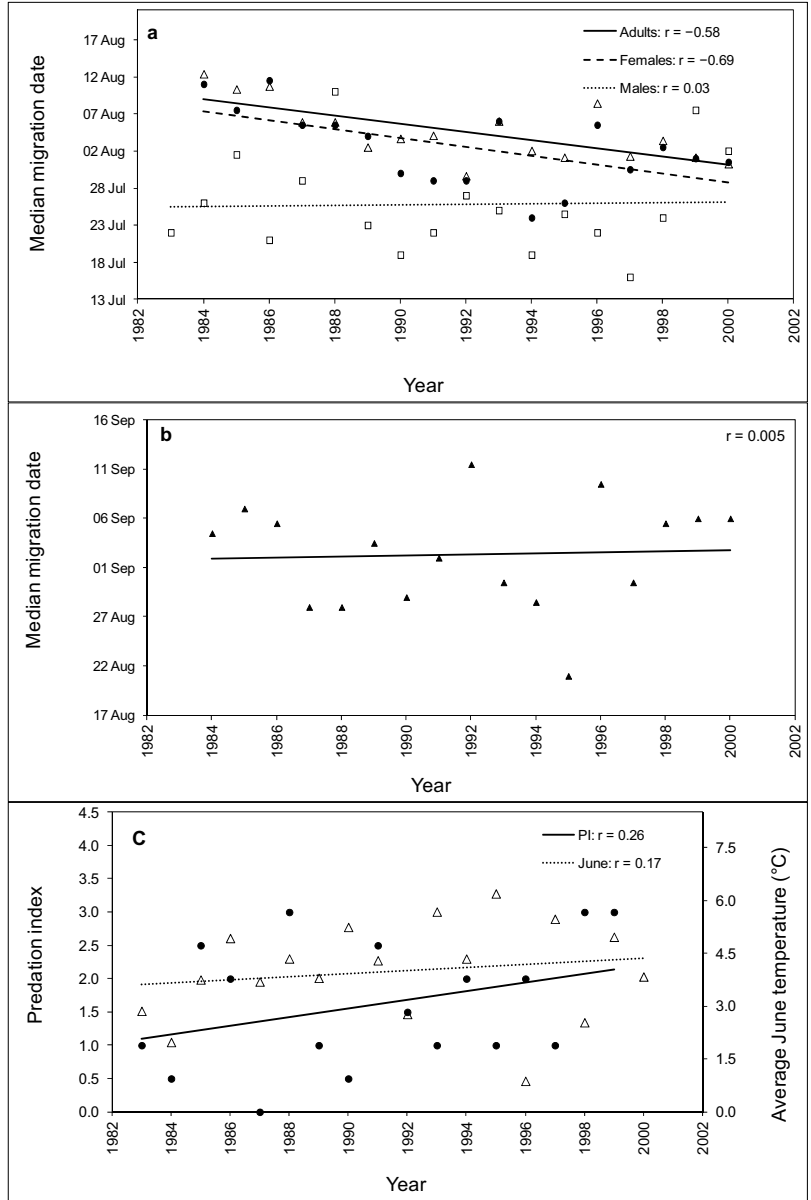


Fig. 3. Median migration dates of all adults, males and females (a) and juveniles (b) of Curlew Sandpipers passing through northern Poland (1983–2000). In (a) solid black circles = all adults, open triangles = females, and open squares = males. Panel (c) shows the trend in predation index (PI) and average June temperature (June) in the Taimyr Peninsula in the Siberian Arctic region (1983–2000). Predation index is obtained from Blomqvist *et al.* (2002), and data on June temperature in the Arctic region are from the National Oceanic and Atmospheric Administration (NOAA).

### 3.4. Trends in migration dates

Both predation index ( $F_{1,678} = 4.77, P = 0.005, b = -1.16$ ) and June temperature ( $F_{1,678} = 14.64, P = 0.002, b = 1.25$ ) were significant predictors of the observed numbers of migrants during 1984–2000, but not July temperature ( $F_{1,678} = 2.02, P = 0.184, b = -0.99$ ). There was also a significant interaction between predation index and June temperature ( $F_{1,674} = 6.13, P = 0.02, b = -2.98$ ). After control-

ling for the annual variation in predation pressure and June temperature, there was a significant and negative trend in the median migration date of adults during 1984–2000 ( $F_{1,686} = 7.68, P = 0.001, b = -0.59$ ; Fig. 3).

There was no significant trend in the median migration dates of males ( $F_{1,606} = 2.72, P = 0.099, b = -0.145$ ) but there was for that of females during 1983–2000 ( $F_{1,468} = 8.461, P = 0.003, b = -0.28$ ). The interaction between year and sex was signifi-

cant ( $F_{2,1073} = 4.449, P = 0.001$ ), suggesting that the general migration trend was driven by females. There was no significant trend in the median migration dates of juveniles over the period of 1983–2000 ( $F_{1,332} = 0.38, P = 0.53, b = -0.07$ ).

#### 4. Discussion

The relationship between the timing of migration of adult Curlew Sandpipers with predation and temperature in the Arctic breeding ground is consistent with the observations of Figuerola (2006), Meissner (2005, 2006) and Soloviev and Tomkovich (2006). Generally, adults migrated earlier in years with high predation pressure (and hence low breeding success) and when June temperatures were lower than average. The significant interaction between breeding success and predation indicates that the difference in timing of migration between good and poor breeding years was pronounced in years of high predation pressure. This implies that, in the Curlew Sandpiper, breeding success is not always determined by predation on eggs and chicks. Heavy snow storms, floods and other extreme weather conditions can result in mortality of chicks (Reports from the Arctic Birds Breeding Conditions Survey 1984–2008). However, only poor breeding success resulting from high predation pressure had a significant impact on the timing of migration in adult birds.

The link between predation and the timing of migration has been previously suggested in shorebirds. The Predation Danger Hypothesis (Niehaus & Ydenberg 2006), for example, explains why some shorebirds adjust aspects of their annual schedules (breeding, moult or migration) to limit the amount of time they are exposed to the danger posed by predators, such as the Peregrine Falcon *Falco peregrinus* and other raptors either on the breeding grounds or on the migratory route.

Juveniles migrated later in years of high than in years of low predation pressure. These late-migrating juveniles might be the result of re-nesting attempts. In years of high predation pressure, when nests at southern breeding grounds are depredated, some individuals may move northward where the late snowmelt allows them to set up new territories (Tomkovich & Soloviev 2006). Such a situation was demonstrated in the Sanderling

*Calidris alba* in the High Arctic northern Taimyr (Tomkovich & Soloviev 2001). Under the double-clutch breeding system, one-third of the population may attempt to produce second clutches if breeding starts early, but in late breeding seasons or in years when clutches are depredated late in the season, virtually no second clutches are laid (Tomkovich & Soloviev 2001).

The timing of migration of adult females occurred about 12 days later than males, but when breeding failed females migrated earlier than in successful breeding years (see Figuerola 2006). A similar pattern has been described in the Wilson's Phalarope *Phalaropus tricolor* (Jehl 1987) and the Wood Sandpiper *Tringa glareola* (Remisiewicz & Wennerberg 2006). In all of these species, males migrate on average earlier than females do.

The migration of males and females may be affected by different factors on the breeding grounds. The temperature in June had the strongest influence on the timing of migration in males, whereas in females predation pressure and July temperature were more important. Males are not involved in parental care, so the timing of their migration would be determined by how early or late the breeding starts. Warm weather in June decreases snow cover and increases food availability (Summers & Underhill 1996, Meltofte *et al.* 2006), facilitating early egg-laying and consequently early departure of males from the breeding grounds. On the other hand, the migration of females will depend mostly on the success of the breeding attempt which is influenced by predation pressure (Underhill *et al.* 1989) and by the time allocated to the young to become independent (Soloviev *et al.* 2006), which is in turn affected by July temperature (Schekkerman *et al.* 1998).

The overall timing of migration of adults became earlier over the years by a factor of  $-0.59$  days/year, which translates into an average advancement of the median migration date by 10 days from 1983 to 2000. Advancement in the timing of autumn migration can be due to the advancement in breeding season (Bairlein &

Winkel 2000, Sokolov *et al.* 1998). However, the lack of a directional trend in juveniles suggests that the start of breeding in this species, and the duration of juveniles' development, have remained unchanged. Another possibility is that the breeding season of the Curlew Sandpiper is being cut

short due to the increasing frequency of failed breeding attempts, causing the adults to leave the breeding grounds earlier.

Three findings support the hypothesis that the frequency of breeding failures significantly affects the timing of migration. Firstly, there was a significant and negative trend in the number of juveniles observed at the present study sites in Poland over the study years. Secondly, both predation pressure and June temperature significantly determined the median migration date in adults. The significant interaction between predation pressure and June temperature also suggests that increasing temperature may have amplified the effect of predation on the trend in the timing of migration. Thirdly, Kausrud *et al.* (2008) showed that the warming climate may have disrupted lemming cycles, resulting in fewer lemming outbreaks in the tundra. In accordance with the lemming-bird hypothesis (Roselaar 1979, Summers 1986, Summers & Underhill 1987), this decline in lemming abundance can result in predators to switch from preying on lemmings to increasingly prey on eggs and young of shorebirds. The result would be an earlier departure of adult birds from the breeding grounds.

The main conclusion of this study is that the timing of migration in the Curlew Sandpiper on non-breeding areas was affected by temperature and predation on their breeding grounds. The indirect effect of climate on predator-prey cycles may have caused the trend in earlier departures from the breeding areas in the Curlew sandpiper. For such migratory species, the timing of migration must coincide with periods of food availability on the migration route and on non-breeding grounds. This study supports the idea that the timing of migration can be used to infer conditions on the breeding grounds, at least in migratory Arctic breeding birds.

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## Kuovisirrin muuton ajoittuminen Puolassa riippuu arktisten pesimäseutujen olosuhteista

Muuton ajoittumisen viimeaikaiset siirtymät on joillakin kahlaajalajeilla liitetty ilmaston vaihteluun. Eri lajien erilaiset vasteet syysmuuton ajoittumisessa kuitenkin viittaavat siihen, että ilmaston ohella myös jotkin muut tekijät voivat olla taustalla.

Tässä työssä määritettiin vakionäytteenotolla muuton ajoittumisen syitä kuovisirrillä (*Calidris ferruginea*) Puolassa. Aikuisten ja nuorten muuton ajoittumiseen vaikutti pesimämenestys, mikä vuorostaan oli yhteydessä arktisten pesimäseutujen saalistuspaineeseen ja kesä–heinäkuun keskilämpötiloihin. Vanhojen lintujen mediaanimuuttopäivä oli merkitsevästi myöhäisempi hyvinä kuin huonoina pesimävuosina. Jokaista yhden celsiusasteen arktisen alueen kesäkuun keskilämpötilan nousua kohti muutto aikaistui 2,3 päivällä. Nuorten yksilöiden mediaanimuuttopäivä korreloi positiivisesti saalistuspaineen ja negatiivisesti arktisten seutujen kesäkuun lämpötilan kanssa. Mediaanimuuttopäivä aikaistui aikuisilla 0,59 päivää vuotta kohti, mikä tutkimusjaksolla 1984–2000 tarkoittaa kymmentä päivää.

Tulokset viittaavat siihen, että pesimäseutujen olosuhteet voivat vaikuttaa elinkierron vaiheiden ajoittumiseen. Ilmastonmuutos lienee lisännyt nuoriin kuovisirreihin kohdistuvaa saalistusta, mikä vuorostaan lisää huonojen pesimävuosien osuutta ja vaikuttanee lajin syysmuuton ajoittumiseen.

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