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Impact of Climate and Predation on Autumn Migration of the Curlew Sandpiper

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Abstract.—Using constant-effort catch data, causes of annual variation in the timing of migration of Curlew Sandpipers (*Calidris ferruginea*) migrating through Ottenby, Sweden, as well as the trend in timing of migration from 1946-2005, was investigated. Variation in the timing of autumn migration of adult and juvenile Curlew Sandpipers was influenced by breeding success connected to predation pressure on the Arctic breeding grounds. Median migration date of adult birds was significantly later in good breeding years compared with poor breeding years while the migration of juveniles was earlier in good breeding years compared with poor breeding years. Also, adults migrated earlier when the average temperature in June was warmer. Median migration dates of adults have advanced by 23 days from 1946-2005, but the migration dates of juveniles have remained unchanged. Unchanged migration dates of juveniles indicate that earlier departure of the adult Curlew Sandpipers from the breeding grounds was not due to earlier breeding. Evidence suggests that declining breeding productivity as a result of increasing predation on broods of shorebirds might, over the years, be the reason for the observed pattern of early departure of adults from the breeding grounds. One possible consequence of earlier migration is a mismatch between timing of migration and periods of food abundance on migration routes and at the wintering grounds, leading to a decline in adult and juvenile survival and population size. Received 24 February 2010, accepted 30 September 2010.

Key words.—Arctic, breeding success, *Calidris ferruginea*, Curlew Sandpiper, June temperature, Ottenby, migration, phenology, predation.

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Migration is a critical event in a bird's life cycle and must be timed to coincide with periods of food abundance (Thomas 1979; Fransson *et al.* 2008; Newton 2008). A mismatch between the migration period and food abundance along the migratory route will reduce a migrant's prospects of survival (Both *et al.* 2006; Møller *et al.* 2008; Reif *et al.* 2008). Also, a shift in the timing of the post-breeding migration can affect subsequent events in the bird's life cycle. For example, many shorebirds molt their flight feathers only after arriving at the non-breeding ("wintering") area (Ginn and Melville 1983; Hayman *et al.* 1986; Underhill 2003), which suggests that the timing of molt could shift in response to the timing of migration.

Climate change has already led to changes in the phenology of migration in many shorebird (wader) species (e.g. Mason 1995; Sparks 1999; Jenkins and Watson 2000; Hüppop and Hüppop 2003; Both *et al.* 2005). Earlier spring migration and arrival at the breeding grounds, enabled by milder winters, has resulted in many species breeding earlier in Europe and North America (e.g. Crick *et al.* 1997; Forchhammer *et al.* 1998; Brown *et al.* 1999; Crick and Sparks 1999). Earlier breeding should then also result in the birds leaving the breeding grounds earlier since shorebirds migrate as soon as they are free of parental responsibilities (Tomkovich and Soloviev 2006).

Among shorebirds, earlier, later or unchanged migration trends have been described. For instance, the timing of the southward migration through Europe has advanced in Wood Sandpiper (*Tringa glareola*), Common Sandpiper (*Actitis hypoleucos*) and Dunlin (*Calidris alpina*), has been delayed in Ruff (*Philomachus pugnax*), Snipe (*Gallinago gallinago*) and Little Ringed Plover (*Charadrius dubius*), but has not changed in Little Stint (*C. minuta*) and Green Sandpiper (*Tringa ochropus*) (Anthes 2004; Adamik and Pietruszkova 2009). These divergent patterns suggest that changes in the timing of autumn migration cannot be attributed solely to climate change.

In shorebirds, the timing of autumn migration depends largely on the end of the reproductive season. Adults can depart from the breeding grounds after they have completed breeding or if they lose their broods (Tomkovich and Soloviev 2006). Hence, environmental conditions can influence the time when breeding starts and the success of shorebirds' nesting attempts, and thus the time when post-breeding migration starts. Snow cover when birds arrive can delay egg-laying (Green *et al.* 1977; Summers and Underhill 1996), low temperatures can reduce the abundance of insect prey delaying egg-laying (Meltofte *et al.* 2006), and wind chill can interfere with mating and the incubation of eggs (Tomkovich 1995). Heavy snowfall, storms, floods, or the trampling of nests by reindeer (*Rangifer tarandus*) during the breeding season can cause the loss of clutches (Arctic Breeding Birds Survey). In shorebirds, such as Curlew Sandpiper (*Calidris ferruginea*), Sanderling (*Calidris alba*), and Turnstone (*Arenaria interpres*), predation on eggs and young also influences breeding success (Summers and Underhill 1987; Underhill *et al.* 1989). Predators such as Arctic Fox (*Alopex lagopus*) and other predators that prey primarily on lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) switch their diet to the eggs and chicks of shorebirds in years of low rodent abundance (Summers *et al.* 1998; Underhill *et al.* 1993).

We chose the Curlew Sandpiper as a model species of migrant shorebird breed-

ing in the Arctic to examine how environmental conditions on the breeding grounds can affect the timing of autumn migration. Curlew Sandpipers breed in the high Arctic tundra between 71°40'E-156°40'W and 67°05'-77°23'N (Holmes and Pitelka 1964; Lappo and Tomkovich 2006). The species arrives in the Taimyr Peninsula in June (Syroechkovski and Lappo 1994) and egg-laying starts between 15-22 June (Tomkovich and Soloviev 2006). Only the females incubate. Males leave their territories soon after the females begin incubating and start migrating southwards by early July, while the females migrate after the young have fledged or when breeding fails (Holmes and Pitelka 1964; Tomkovich 1988). Therefore, adults are observed at stopover sites in two waves, the first formed mainly of males and the second mainly of females (Diadicheva and Khomenko 2006; Meissner 2006; Morozov 2006).

Blomqvist *et al.* (2002) and Figureola (2006) showed that the timing of adult Curlew Sandpipers migration was linked to predation in the Arctic and the proportion of juveniles in the total number of birds observed, respectively. In the Curlew Sandpiper, reproductive success (measured as the proportion of juveniles) is related to predation in the Arctic (Summers *et al.* 1998; Underhill *et al.* 1993; Blomqvist *et al.* 2002). Also, Schekkerman *et al.* (1998) described a relationship between the breeding productivity of the Curlew Sandpiper and the temperature in the Arctic; low temperature in the Arctic during the breeding season resulted in low breeding success.

Whether temperature in the Arctic affects the timing of shorebirds' southwards migration, and what the mechanism might be, has yet to be explored. Temperature could directly affect the timing of breeding, and thus of departure, or indirectly influence breeding success. Males and females differ in their involvement in parental care, and the juveniles are only ready to leave the breeding grounds about a month after adults, so temperature and breeding success could act differently on the migration timing of each of these sex and age groups. The aim

of this study is to test the direct and indirect effects of weather and predation during the breeding season on the timing of migration for the adult males and females as well as for the juveniles. We also attempt to determine the mechanism by which climate change might have affected trends in the timing of migration for these Arctic-breeding shorebirds over the past 60 years. We hypothesize that: 1) temperature and predation affect the timing of migration of adults and juveniles; 2) conditions on the breeding grounds will affect males and females differently because of the Curlew Sandpiper's system of parental care; and 3) climate change will affect long-term trends in the timing of Curlew Sandpiper migration.

METHODS

Ring data on Curlew Sandpipers were obtained from Ottenby Bird Observatory (56°12'N, 16°24'E; Fig. 1) on the island of Öland in the Baltic Sea at the southern tip of Sweden, where annual observations and ringing have been carried out since 1946 (Edelstam 1972; Hedenström 2004). Birds were captured from early July to late October/early November, the entire autumn migration period of the Curlew Sandpiper (for details see Hedenström 2004; Helseth *et al.* 2005; Stervander *et al.* 2005). Walk-in funnel traps (Bub 1991) were set in rotting seaweed at the shoreline of the southern point of Öland. The traps were checked and emptied every hour, from approximately one hour before dawn to about one hour after dusk.

Curlew Sandpipers have been aged since 1946 based on differences in plumage between adults and juveniles (Prater *et al.* 1977). From 1990 onwards, the following measurements were made: the maximum wing length

(Svensson 1992) to the nearest 1 mm, total head length from the bill tip to the back of the skull (Green 1980) to the nearest 1 mm, and body mass to the nearest 0.1 g.

Data Analysis

Adult birds were sexed using the discriminant function formula $D = 0.07815 \cdot W + 0.47962 \cdot B - 28.7302$; D = discriminant score where $D < 0$ = males, $D > 0$ = females, W = wing length, and B = bill length (Wymenga *et al.* 1990). The histogram of bill lengths of sexed birds shows two clearly separated modes, indicating there was little misclassification of males and females. The bill lengths of the sexes overlapped between 37–39 mm, so birds within this range were excluded from analyses of the migration timing of the sexes.

The annual median dates of migration were computed separately for adults and juveniles. The percentage of juvenile birds in the total annual catch was used as a measure of breeding success (Minton *et al.* 2005), a method widely used as an indicator of breeding performance especially in species that use well-defined migration route and/or wintering areas (Boyd and Piersma 2001; Møltøfte 2001; Beale *et al.* 2006). Because breeding success in the Curlew Sandpiper usually exhibits a “boom-or-bust” pattern (Summers *et al.* 1998), years when juveniles constituted more than 20% of the total catch were classified as good breeding years and years when juveniles constituted 13% or less of the catch were classified as poor breeding years (Summers and Underhill 1987; Schekkerman *et al.* 1998).

How the timing of migration was affected by temperatures and predation in the Arctic was examined using general linear models (GLM). The annual median migration date was the dependent variable, with breeding success (good or poor) as fixed factor, and annual June average temperature and the predation index as covariates. Data on average June temperature in the Arctic (Polyakov *et al.* 2002) was used as a proxy for weather conditions on the breeding grounds during the egg-laying period since most Curlew Sandpiper clutches are completed during 15–22 June (Tomkovich and Soloviev 2006). The index of predation pressure provided by Blomqvist *et al.* (2002) was used to analyze the effects of predation on migration. The index of predation is the likelihood that wader nests and chicks will be depredated, with scores from 0 (low predation pressure) to 3 (high predation pressure).

The overall migration pattern, derived from daily catches, was compared between poor and good breeding years separately for males and females. We combined the data from all years classified as good breeding years and did the same for poor years, and used the Kolmogorov-Smirnov test to reveal if the “waves” of migration of the different sexes differ in good and poor breeding years.

We examined the trend for the median migration dates of adult and juvenile birds over the past 60 years using general regression models. The annual median migration dates was the dependent variable, the index of predation and the average June temperature in the Arctic were covariates, and the model included second-order interactions of the variables. The model with the lowest Akaike Information Criterion (AIC) was selected as the final best-fitted model. The slope (b) provided the measure of the magnitude and the direction of the trend. We used Statistica 8.0 software (Statsoft Inc. 2008) for all statistical analyses.

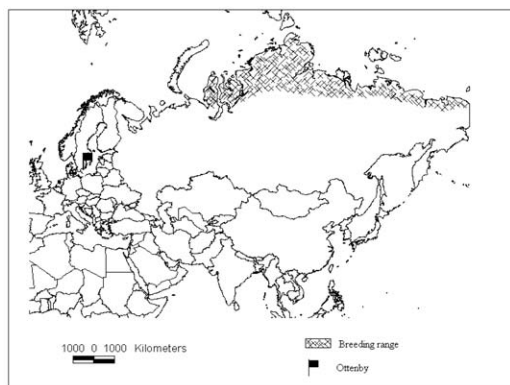


Figure 1. Breeding range of the Curlew Sandpiper (adapted from Cramp and Simmons 1983; Lappo and Tomkovich 2006) and location of Ottenby Bird Observatory, Sweden.

RESULTS

Through 1946-2005 the Ottenby station banded 5,854 Curlew Sandpipers, with annual totals ranging from one (1968 and 2002) to 623 (1999). There was no significant trend in the yearly number of birds banded at Ottenby over the past 60 years (linear regression: $\beta = 0.37$, $p = 0.62$, $N = 60$). Forty-one years were classified as good breeding years and 18 as poor breeding years. In 1946 - 1975 there were six poor breeding years, in 1976-2005 there were twelve.

Migration Pattern of Adults

The median migration date of adult birds in good breeding years was 4 August (inter-quartile range: 26 July-13 August), significantly later than the median migration date of 25 July in poor breeding years (inter-quartile range: 20 July-02 August; GLM: $F_{1,57} = 9.20$, $p < 0.01$). Median migration dates occurred earlier in years of high predation than in years of low predation (GLM: $F_{1,34} = 6.18$, $p = 0.01$, $\beta = -2.66$; Fig. 2). Also, birds migrated significantly earlier when the average temperature in June was warmer than colder years, on average 2.8 days earlier for every 1°C rise in temperature ($F_{1,57} = 4.97$, $p = 0.03$, $\beta = -2.76$; Fig. 3). The interaction of breeding

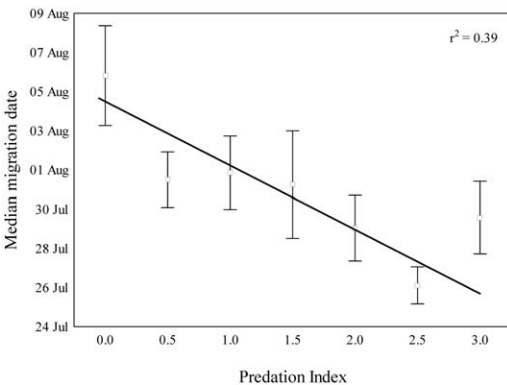


Figure 2. Relationship between the median migration date of adult Curlew Sandpipers passing through Ottenby, Sweden and index of predation in the Arctic ($p < 0.01$, slope = -2.66). White square is the mean migration date with given predation index, whiskers represent 95% confidence intervals, and the solid black line is the regression line.

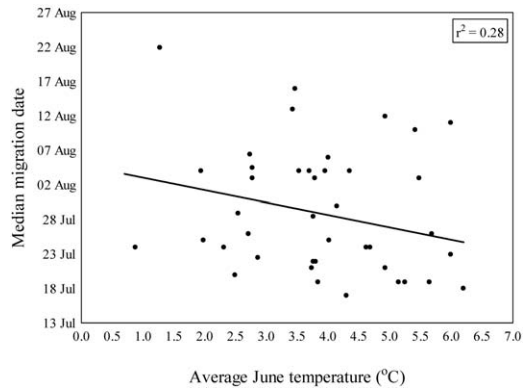


Figure 3. Relationship between the median date of migration of adult Curlew Sandpipers through Ottenby, Sweden with the average June temperature in the Arctic ($p < 0.01$, slope = -2.76)

success and June temperature was not significant ($F_{1,57} = 0.05$, $p = 0.81$), but the interaction of breeding success and the predation index was ($F_{1,37} = 2.16$, $p = 0.01$), indicating that as predation pressure increases, the difference between the timing of migration in good and poor breeding years becomes more pronounced.

The median migration date of males in good breeding years was 19 July (inter-quartile range: 17 July - 06 August), which was not significantly different ($F_{1,57} = 0.10$, $p < 0.901$) from the median migration date in poor breeding years on 21 July (inter-quartile range: 18 July-25 July). However, the males' pattern of migration differed significantly between good and poor breeding years (Kolmogorov-Smirnov test: $D_{1,447} = 0.25$, $p = 0.02$). The date of the maximum difference in the cumulative percentage of birds that had migrated through Ottenby in good and poor years was 31 July. In good breeding years 66% of the observed birds had migrated by this date, but in poor years 88% of the birds had migrated (Fig. 4). The median migration date for females in good breeding years was 10 August (inter-quartile range: 3 August-15 September) which was significantly later ($F_{1,57} = 7.61$, $p = 0.02$) than the median migration date in poor breeding years on 23 July (inter-quartile range: 20 July-29 July). There was also a significant difference in the females' pattern of migration in good and poor breeding

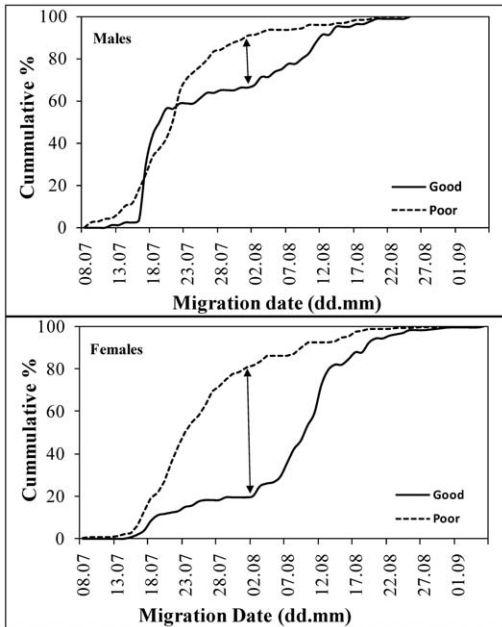


Figure 4. Cumulative curve of the daily proportion of numbers of male (upper figure) and female (lower figure) Curlew Sandpipers passing through Ottenby, Sweden, illustrating the difference in the phenology of migration in good (—) and poor (...) breeding years. Arrow shows the date when maximum difference in the phenology occurs.

years (Kolmogorov-Smirnov test: $D_{1,468} = 0.61$, $p < 0.01$, Fig. 4). The date of the maximum difference in the cumulative percentage of birds recorded on migration in good and poor breeding years was 1 August. By this date, 19% of females recorded in good breeding years had migrated but 86% of females had migrated in poor breeding years.

Between 1946-1995 median migration dates advanced by an average of 23 days, a significant trend ($F_{1,78} = 16.72$, $p < 0.01$, $\beta = -0.39$, Fig. 5). Both the average June temperature ($F_{1,78} = 18.56$, $p < 0.01$, $\beta = -3.33$) and the predation index ($F_{1,78} = 7.83$, $p = 0.01$, $\beta = -2.26$) were significant predictors of this trend.

Migration Timing of Juveniles

The median migration date of juvenile birds in good breeding years was 31 August (inter-quartile range: 27 August-7 September), significantly earlier than the median migration date of 10 September in poor breed-

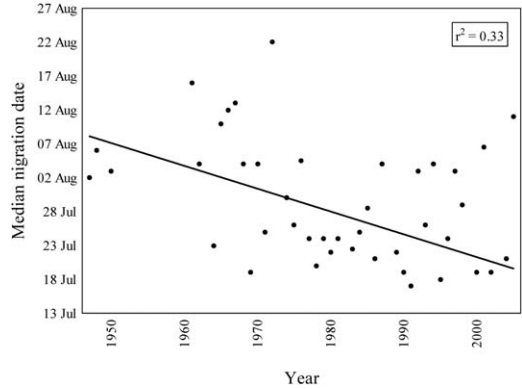


Figure 5. Trend in the median migration dates of Curlew Sandpipers passing through Sweden (1946-2005) on autumn migration.

ing years (inter-quartile range: 2 September-17 September; $F_{1,54} = 14.31$, $p < 0.01$). Juvenile birds migrated significantly earlier in years with a low predation index compared with years with a high predation index ($F_{1,39} = 8.66$, $p = 0.01$, $\beta = 4.46$; Fig. 6). Their migration timing was not affected by average June temperature in the Arctic ($F_{1,39} = 0.25$, $p = 0.62$, $\beta = 0.58$). There was no significant trend in the median migration dates of juvenile birds over the years ($F_{1,32} = 0.38$, $p = 0.53$, $\beta = -0.07$).

DISCUSSION

The autumn passage of adult Curlew Sandpipers through their stopover sites in

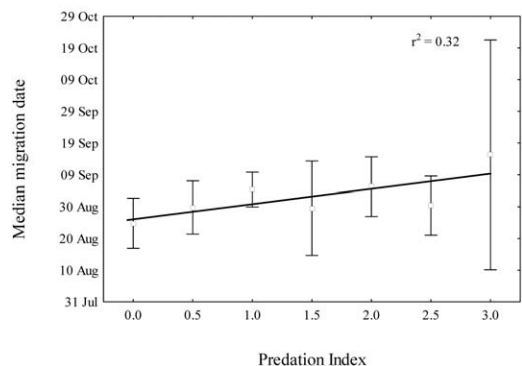


Figure 6. Relationship between the median migration date of juvenile Curlew Sandpipers passing through Ottenby, Sweden and index of predation in the Arctic ($p < 0.01$, slope = 4.46). White square - mean, whiskers - 95% confidence intervals, dashed line - regression line.

Europe usually has a bimodal pattern, with the males observed about 10-15 days ahead of females (Diadicheva and Khomenko 2006; Meissner 2006; Morozov 2006). Our results also showed an earlier passage of males through Ottenby compared to females, but the difference in the median migration dates of the sexes was smaller in poor breeding years (three days) than in good breeding years (20 days). The reason could be that in years of poor breeding success when many clutches are lost due to high predation, the females leave the breeding grounds soon after the males. Since most males leave the breeding ground soon after the eggs have been laid, many females have no opportunity to lay a replacement clutch when the first one has been depredated. But in years with low predation and good breeding success, the females stay with their chicks and thus depart from the nesting grounds later than in years with high predation (Figueroa 2006).

The significant interaction of breeding success and the predation index shows that predation pressure is the main factor determining the difference in the timing of adult birds' migration (both sexes combined) between good and poor breeding years. Our findings accord with the results of Summers *et al.* (1998), Blomqvist *et al.* (2002) and Figuerola (2006). However, our study also shows that the average June temperature in the Arctic contributes to the inter-annual variation in the timing of migration and that adults migrate earlier in warmer years. The variation in migration dates could be an effect of a delay in breeding caused by cold weather at the breeding grounds. Shorebirds are "capital breeders" and depend on the food available at the breeding grounds to provide the nutrients they need for egg formation (Klaassen *et al.* 2001; Morrison and Hobson 2004). Egg-laying is delayed if cold weather limits the abundance of surface arthropods when the birds arrive at their breeding areas (Møtøfte *et al.* 2006) or if the ground is still covered by snow (Green *et al.* 1977; Summers and Underhill 1996). The delay would therefore also delay the post-breeding migration.

The median migration date of juvenile birds occurred eleven days earlier in good breeding years than in poor years, and this difference was related to the predation index. The explanation could be that, based on predator functional response to prey abundance (Solomon 1949; Lack 1954), in years with high predation, and thus poor breeding success, more clutches laid early in the season are depredated, but the later clutches might have higher a chance of survival. As a result, juvenile migration would occur later than in years of low predation.

Our results showed that both the average temperature in June and predation pressure in the Arctic contributed significantly to the trend towards earlier migration in adult Curlew Sandpipers. Shorebirds such as Wood Sandpiper, Common Sandpiper and Dunlin show a similar trend towards earlier autumn migration in response to global warming (Adamik and Pietruszkova 2009; Anthes 2004), which has been attributed to the advancement of the breeding season (Zack and Liebezeit 2008). However, the relationship between the migration timing of the Curlew Sandpiper and the June temperature might not be caused by advancing breeding seasons for two reasons. Firstly, the early migration of both adults and juveniles is a pattern that would be seen in years of early breeding (Sokolov *et al.* 1998). We found no trend over the 60-year period towards earlier migration in juvenile birds corresponding to that observed in the adults. Secondly, studies have reported no temporal trends in the first arrival dates of waders in the Taimyr Peninsula or in the Yukon-Kuskokwim Delta, despite a significant spring warming trend (Møtøfte *et al.* 2007).

Thus, we might consider an alternative scenario suggested by Ims and Fuglei (2005) and Kausrud *et al.* (2008) that climate change has led to fewer lemming outbreaks in the tundra. Fewer lemmings would cause predators such as the Arctic Fox (*Alopex lagopus*) and the Snowy Owl (*Bubo scandiacus*) to prey more on the eggs and chicks of shorebirds, which would decrease their breeding productivity. Our results showed six poor breeding years from 1946-1975 but from

1976-2005 the number of poor breeding years increased to eleven. Also, other papers provide more evidence of the increasing predation pressure on the Curlew Sandpiper (Blomqvist *et al.* 2002) and declining breeding productivity in the species (Meissner 2006). The number of juvenile Curlew Sandpipers observed at non-breeding grounds in Australia (Minton *et al.* 2005; Gosbell and Clemens 2006) and South Africa (Harebottle and Underhill 2006) has also declined over the years. Based on our results which indicated that adult the Curlew Sandpiper migrated earlier migrated in poor breeding years, we suggest that the trend towards earlier migration from 1946 to 2005 is due to poor reproductive success. However, without further research, it would be difficult to pinpoint one major cause for the poor breeding success of the Curlew Sandpiper. The reasons could be varied, from a mistiming of the reproductive period outside the peak of insect abundance (Visser *et al.* 2004; Tulp and Schekkerman 2008), to an alteration of the breeding habitat resulting from climate change (Meltotte 2007).

The consequences of the earlier southwards migration on the population of the Curlew Sandpiper are difficult to predict but asymmetric climate change at temperate and tropical latitudes could result in a mistiming of the migration and the peak food abundance en route or at the non-breeding grounds (Houghton *et al.* 1995; IPCC 2007) which would lead to higher mortality of migrants after they leave the breeding grounds. Combined with low breeding success, the increasing mortality could considerably reduce the population size. Jones and Cresswell (2010) examined the population trends of 134 species of migratory birds and showed that populations that experience a greater rate of warming at their breeding grounds than at their wintering grounds are more likely to be in decline.

In conclusion, we suggest that increased frequency of poor breeding years in 1976-2005 than during the preceding 30 years, caused by the increased predation on shorebird clutches due to less frequent lemming outbreaks have led to earlier southwards mi-

gration from the breeding ground by Curlew Sandpipers. The link between climate change, the decreasing abundance of lemmings and increased predation on shorebird clutches needs to be tested on other species whose breeding success is also affected by predation. The potential conservational implication is that the Curlew Sandpiper and probably other Arctic-breeding migrant shorebirds could be facing a serious decline due to the long-term effects of climate change on their reproductive output. Effects of climate change on the population of these shorebirds could be ameliorated by the preservation and management of their stopover and wintering sites to increase the migrants' survival rates outside their breeding grounds.

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