

Sven Blomqvist · Noël Holmgren · Susanne Åkesson
Anders Hedenström · Jan Pettersson

Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden

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Abstract The bird–lemming hypothesis postulates that breeding success of tundra-nesting geese and waders in Siberia follows the cyclic pattern of lemming populations, as a result of predators switching from lemmings to birds when the lemming population crashes. We present 50 years of data on constant-effort catches of red knot *Calidris canutus* and curlew sandpiper *C. ferruginea* at an autumn migratory stopover site (Ottenby) at the Baltic Sea, supplemented with literature data on winter censuses of dark-bellied brent goose *Branta b. bernicla* and white-fronted goose *Anser albifrons* in northwestern Europe, and waders in Germany and Southern Africa. Number and proportion of juveniles in these bird populations (both our own and literature data) were compared with an index of predation pressure (calculated from the abundance of lemmings on the Taimyr peninsula), and climate indices for the North Eurasia and the North Atlantic regions. The index of predation pressure correlated significantly with the number of juveniles of red knot and curlew sandpiper, but not with number of adults. Also, this index correlated with the reproductive performance of geese and waders reported in the literature. Fourier analysis revealed a significant deviation from random noise with the maximum spectral density at the period length of 3 years for number of juvenile red knots and curlew sandpipers captured at Ottenby, abundance of lemmings, reproduction in arctic fox *Alopex lagopus*, and reproductive

performance in geese on the Siberian tundra. Also, the date of passage at Ottenby for adult red knot and curlew sandpiper showed a spectral density peak at a period length of 3 years, the latter species also showing a peak at a period length of 5–6 years. Passage dates for adult red knot and curlew sandpiper were earlier in years of high predation pressure compared with years of low predation pressure. The fluctuations in reproductive success of the studied Siberian goose and wader species appear to be primarily influenced by biotic factors in the breeding area, rather than by abiotic factors, such as climate oscillations. Annual variations in migratory arctic bird populations may have far reaching effects in habitats along their migration routes and in their wintering areas. We suggest a link between lemming cyclicity in the Northern Hemisphere and predation pressure on Southern Hemisphere benthos, in which the signal is carried between continents by long distance migrating waders.

Keywords Bird–lemming hypothesis · Climate oscillation · Population dynamics · Predation · Prey switching

Introduction

It has been suggested that lemmings indirectly affect the reproductive output of tundra-breeding geese and waders. According to the bird–lemming hypothesis (emerging from Roselaar 1979; Summers 1986), the breeding of these ground-nesting birds is successful when lemming populations increase or stay high, but poor in years immediately after lemming peaks, when lemmings are scarce, but their predators are still abundant (Dhondt 1987; Summers and Underhill 1987; Summers et al. 1998; for review, see Greenwood 1987; Sutherland 1988). This hypothesis assumes that in lemming-poor years, predators such as arctic fox *Alopex lagopus* and mustelids *Mustelidae* switch from feeding on lemmings to eggs and young of birds.

The causes of the fluctuations in goose and wader reproduction on the Siberian tundra have been widely debated (Boyd 1987; Dhondt 1987; Ebbinge 1987; Owen 1987;

S. Blomqvist
Department of Systems Ecology, Stockholm University,
106 91 Stockholm, Sweden

N. Holmgren (✉)
Department of Natural Sciences, University of Skövde,
P.O. Box 408, 541 28 Skövde, Sweden
e-mail: noel.holmgren@inv.his.se
Tel.: +46-500-448607
Fax: +46-500-448699

S. Åkesson · A. Hedenström
Department of Animal Ecology, Lund University,
Ecology Building, 223 62 Lund, Sweden

J. Pettersson
Storgatan 12e, 386 30 Färjestaden, Sweden

de Boer and Drent 1989; Underhill et al. 1993). Inter-annual variation in weather conditions on the breeding grounds has been proposed as a causal factor explaining the variation in breeding success in arctic geese (Boyd 1987; de Boer and Drent 1989; Syroechkovskiy et al. 1991). In support, the summer temperature in Siberia has been reported to correlate positively with the breeding success of geese and waders (Summers and Underhill 1987; Schekkerman et al. 1998). Regarding geese, other factors have also been related to the breeding success, such as body weight at spring departure, and wind conditions during the northward spring migration (Ebbinge 1987, 1989, 1990; Spaans et al. 1993; Ebbinge and Spaans 1995, but see also Underhill and Summers 1990). Direct field observations on Taimyr in the year after a lemming peak suggest that low reproduction in dark-bellied brent geese *Branta b. bernicla* might result from disturbance by wandering arctic foxes causing them to forgo breeding altogether, rather than from predation on eggs and young (Spaans et al. 1998).

The bird–lemming hypothesis originates primarily from observations of curlew sandpiper *Calidris ferruginea* at autumn stopover areas in northwestern Europe (Roselaar 1979). More recently, studies on winter counts of dark-bellied brent goose in northwestern Europe have provided the best evidence so far (Summers 1986; Summers and Underhill 1987; Summers et al. 1998). However, with respect to testing the bird–lemming hypothesis, wader data from autumn migration have several advantages over data obtained from winter counts. First, the population is sampled shortly after the departure from the breeding grounds, whereby the influence of processes affecting the birds outside the breeding season is minimized. Second, the two wader species analyzed in this paper, red knot *Calidris canutus* and curlew sandpiper, migrate to wintering areas in Africa (Smit and Piersma 1989; Piersma et al. 1992), thus experiencing different winter conditions than goose populations wintering in northwestern Europe. Therefore, alternative hypotheses suggesting processes on wintering grounds being responsible for the inter-annual fluctuations in number of juvenile birds can be rejected by analyzing data on these wader species. Third, in waders such as the red knot and the curlew sandpiper, first year birds do not reproduce, but remain in the winter quarters throughout the first summer (Elliott et al. 1976; van Dijk et al. 1990; Summers et al. 1995), while in geese first year birds migrate to the arctic breeding areas, although without reproducing (Ebbinge 1989). Finally, the red knot and the curlew sandpiper considered in the present study have a rather limited breeding range on and near the Taimyr peninsula (Blomqvist et al. 1987; Piersma et al. 1992; Tomkovich and Soloviev 1996), and so may be expected to respond to the same breeding conditions, in contrast to other tundra-nesting bird species, such as the white-fronted goose *Anser a. albifrons*, sanderling *Calidris alba*, and ruddy turnstone *Arenaria interpres*, which have more extended breeding ranges (Cramp and Simmons 1977, 1983).

The bird–lemming hypothesis implies that numbers of juvenile arctic-breeding birds correlate with lemming

fluctuations on the tundra. For adult birds, the bird–lemming hypothesis makes two predictions. First, adult numbers should not correlate with lemming fluctuations. Secondly, in wader species where adults leave the breeding grounds shortly after eggs and young are preyed upon, the adults are expected to migrate earlier in years with high predation pressure on the tundra (typically the year following a lemming peak) than in years with normal or low predation pressure.

In the present paper, we test the bird–lemming hypothesis by using much longer time series (50 years) of Siberian breeding waders than previously available. The data on red knots and curlew sandpipers were collected at an autumn stopover site (Ottenby) at the Baltic Sea, i.e., at an early stage of their southward migration. Also, we test how numbers of adults and juveniles relate to a predation index, based on data from Taimyr, and investigate whether the migratory passage of the adult waders is more advanced in years with high predation pressure than in years with low predation pressure. Moreover, we compiled available literature data on geese and waders to further test the bird–lemming hypothesis. These data include an extended series of counts of white-fronted and dark-bellied brent geese from wintering grounds in northwestern Europe, wader records from an autumn migration site in Germany (Helgoland) and from winter quarters in Southern Africa. Finally, as an alternative to the bird–lemming hypothesis, we investigate whether the breeding success of the studied species correlate with climate oscillations of the North Atlantic Region during autumn and winter, or the North Eurasian Region during spring.

Material and methods

Capturing of waders

Ottenby Bird Observatory (56°12'N, 16°24'E) is located at the southernmost point of the island of Öland, southern Sweden, in the Baltic Sea. Large numbers of migrating arctic birds pass this site when following the Eurasian route of the East Atlantic Flyway (reviewed by Piersma et al. 1987; Smit and Piersma 1989). Migrating waders have been ringed in autumn at Ottenby since 1946 (Svårdsson 1947). Generally, the capture of waders starts in July, as soon as the first migrating waders arrive, and continues until the number of birds in the area is very low in September or October (in a few years also in November). Usually, the trapping is interrupted only by bad weather, but during the periods of 1–15 September 1947, 17–31 August 1948 and 27–31 August 1951 there was no staff at the Observatory.

Red knots and curlew sandpipers were ringed at Ottenby in the time period of 1946–1995 (Appendix 1). The waders were caught in “Ottenby funnel traps” (Bub 1991), i.e., rectangular traps (about 1 m long and made of chicken-wire mesh), with one entrance on each long side. The use of such traps is possible since the tidal range is small (<5 cm) in this part of the Baltic Sea (Magaard 1974). Up to 100 traps were deployed on the banks of decaying seaweed fringing the shores at Ottenby. The traps were checked each hour, except during darkness, when no birds enter the cages. The birds were released after being aged and ringed. Adults could usually be distinguished from juveniles by remnants of their reddish breeding plumage. If adults were in full winter plumage, juveniles were recognized by having buff fringes on wing coverts and comparatively fresh remnants (Witherby et al. 1943; Prater et al. 1977).

Literature data

Population records of lemmings, and estimates of reproductive success in arctic fox, geese and waders on the Taimyr Peninsula, were extracted from the literature (Appendix 2). In Taimyr, the Siberian lemming *Lemmus sibirica* dominates, whereas the collared lemming *Dicrostonyx torquatus* is less abundant. Reported lemming data cover 43 years, and are scored on a four-graded scale (0–3; see Appendix 2 for literature sources) categorized as very low, low, moderate, and high. In a series of data on lemming abundance from 1960 to 2001, a five-graded scale (1–5) was used (Kokorev and Kuksov 2002), but was transformed linearly by us to the range 0–3. We merged the two data sets on lemming abundance by taking the average and rounding to the nearest integer. Then, we calculated an index of predation pressure:

$$I = \frac{(X_{t-1} - X_t + 3)}{2},$$

based on the change in lemming abundance from the previous year (X_{t-1}) to the focal year (X_t). The index ranges between 0 and 3, with 0 representing the minimum and 3 representing the maximum predation pressure (Appendix 2). According to the bird–lemming hypothesis, a decline in lemming numbers from a peak year to the following year is connected to a 1-year lag of maintained high density of predators, which are thereby forced to switch from feeding on lemmings to birds (Dhondt 1987; Summers and Underhill 1987; Summers et al. 1998). In other words, a predation index of 3 is due to maximum decrease in lemming abundance from the previous to the focal year. The proportion of dens occupied by breeding arctic fox in western Taimyr (Kokorev and Kuksov 2002) reflects the reproduction effort of this predator (Appendix 2).

We collected literature data on reproduction in the dark-bellied brent goose and the white-fronted goose based on winter counts in Britain, France (brent goose only) and the Netherlands. These are winter counts of juveniles and adults in the same flocks. The reproductive success is represented by the average proportion of juveniles in wintering flocks, or as the number of juveniles per estimated reproductive adult. The latter measurement was calculated according to Ebbinge (1989), i.e., the proportion of non-reproductive adults (sub-adults) in the focal year was estimated as the proportion of juveniles in the previous year. When data were available from several different counts in the same year, we used the average in our analyses.

Literature data on waders refer to ringing during autumn migration at Helgoland (Germany), and from winter quarters in Southern Africa (Appendix 2). The German data set is given as the total num-

ber of juvenile birds ringed per autumn, whereas the African data set is given as the proportion of juvenile waders ringed each winter.

The used proxies (indices) of climate variation are the Eurasian Pattern [EAP; termed the Eurasia-1 pattern by Barnston and Livezey (1987) and the SCAND by NOAA (2001)] and the North Atlantic Oscillation (NAO), respectively. These climate indices [NAO data downloaded from Mitchell (2001), and EAP data from NOAA (2001)] are known to reflect large-scale changes and circulation anomalies of the atmosphere. The EAP index (available from 1950) refers to a prominent primary circulation centre spanning the Arctic Ocean north of Siberia. Therefore, the EAP index for the month of May was used as an environmental proxy of spring progression on the Siberian tundra, which presumably reflects preconditions for breeding in the studied birds. The NAO dictates climate variability (temperature zonation and precipitation pattern) in the Northwest Atlantic Region, especially during winter (Hurrell 1995). Hence, NAO indices of October to February (available for all years studied) were selected as proxies of autumn and winter conditions in western Europe, to evaluate a possible impact of climate variation in wintering quarters on the proportion of juvenile geese recorded.

Statistical methods

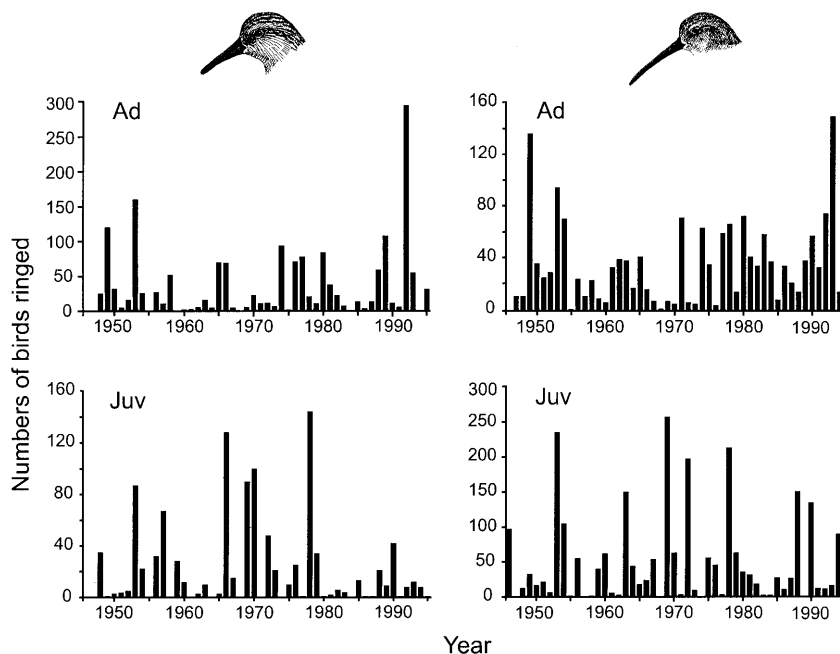
We used the Statistica software package (v 5.0) for the statistical analyses. For test of association, we used the non-parametric Kendall's coefficient (τ) of rank correlation (see Sokal and Rohlf 1995 and Zar 1999). The bird–lemming hypothesis predicts the sign of correlations between lemmings and bird reproduction. Therefore, one-tailed tests were used in these cases. Fourier analyses were undertaken on the time series data to detect cyclic patterns. In these analyses, series length was padded to powers of 2, and data were tapered by 15%. Missing data in the time series were interpolated. The significance of any cyclic pattern was tested by Kolmogorov-Smirnov one-sample test. D-values obtained from the Fourier analysis were evaluated in Table Y (intrinsic model) of Rohlf and Sokal (1995).

Results

Number of waders at Ottenby

From time series analysis (linear regression) of the birds ringed at Ottenby in 1946–1995 (Fig. 1), no significant

Fig. 1 Annual numbers of red knot *Calidris canutus* (left panels) and curlew sandpiper *C. ferruginea* (right panels) captured at Ottenby, Sweden, during 1946–1995. Adults and juveniles are shown separately



trend was revealed in the numbers of adult red knot (slope=0.55, $t_{48}=1.07$, $P>0.05$), juvenile red knot (slope=-0.15, $t_{48}=-0.46$, $P>0.05$), adult curlew sandpiper (slope=0.32, $t_{48}=1.00$, $P>0.05$), or juvenile curlew sandpiper (slope=-0.09, $t_{48}=-0.13$, $P>0.05$). The average number of adult red knot captured was 34 per year (range 0–293), and that of juveniles was 21 (range 0–144, Appendix 1). The average number of adult curlew sandpiper was 34 (range 0–148) and for juveniles 50 (range 0–257). The annual numbers ringed were positively correlated between the two species, both for adults (Kendall $\tau=0.377$, $n=50$, $P<0.001$, one-tailed test) and for juveniles (Kendall $\tau=0.460$, $n=50$, $P<0.001$, one-tailed test). However, in none of the two species was there a positive correlation between the annual numbers of adult and juvenile birds (red knot: Kendall $\tau=0.148$, $n=50$, $P>0.05$; curlew sandpiper: Kendall $\tau=-0.072$, $n=50$, $P>0.05$, one-tailed tests).

Timing of passage and predation pressure

In the red knot, the annual median capture date of adults ranged from 18 July to 11 September, and in the curlew sandpiper from 16 July to 24 August (Appendix 1). On average, adults passed 22 days before juveniles (9 August and 31 August, respectively) in the red knot ($U_{43,40}=202$, $P<0.001$, Mann-Whitney U -test), and 33 days before juveniles in the curlew sandpiper (29 July and 31 August, respectively, $U_{49,47}=14$, $P<0.001$, Mann-Whitney U -test). The range of median capture dates for juvenile red knot was 8 August–19 October, and in the curlew sandpiper 16 August–28 October, respectively.

The timing of the passage in adult red knot and curlew sandpiper appears to be influenced by the breeding success. In fact, a negative relationship was found between the predation index and the median date for the passage of adult red knot (Kendall $\tau=-0.204$, $n=35$, $P<0.05$, one-tailed test), as well as for adult curlew sandpiper (Kendall $\tau=-0.215$, $n=39$, $P<0.05$, one-tailed test). This suggests that in years when many pairs lose their clutches due to predation, the adults leave the breeding grounds to migrate south earlier than in years of successful breeding. In other words, adult birds pass stopover sites along the migratory route earlier in years with low reproductive success (high predation pressure) than in years with high reproductive success (low predation pressure), i.e., in agreement with the bird-lemming hypothesis.

Predation pressure and reproductive success

Arctic foxes reproduce mainly in years with high lemming densities. The proportion of dens occupied by breeding arctic fox correlates with the density of lemmings (Kendall $\tau=0.663$, $n=36$, $P<0.001$, one-tailed test; Fig. 2). If lemming numbers decline sharply from a peak value, the many predators are assumed to feed on eggs

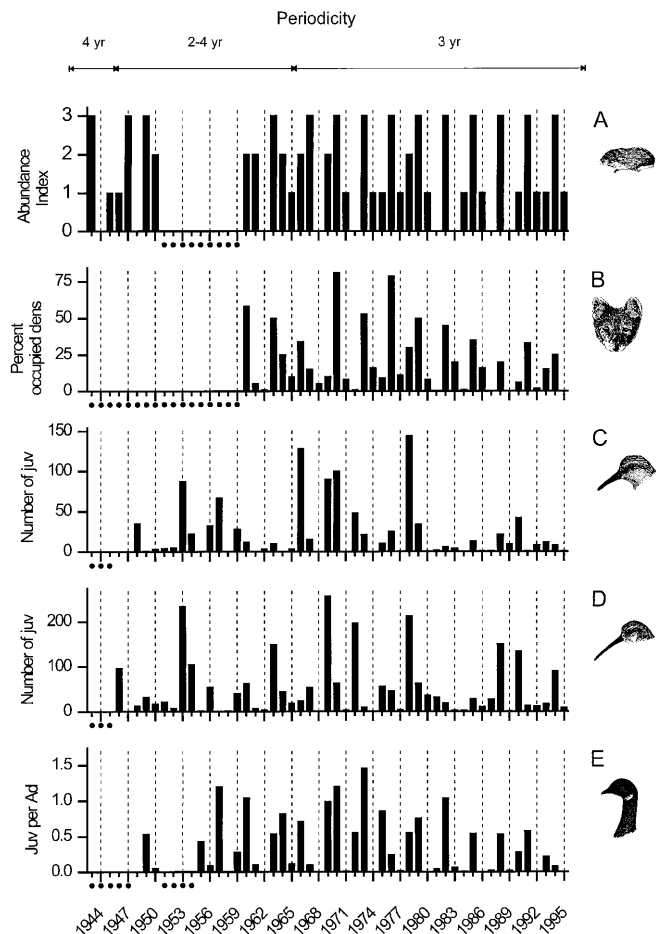


Fig. 2a-e Comparison of time series on population fluctuations in tundra nesting birds and arctic fox with a presumed association with lemming cyclicity. **a** Abundance index (0–3) of lemmings on the Taimyr peninsula, **b** proportion of dens occupied by breeding arctic fox in western Taimyr, **c** number of ringed juvenile red knots during autumn migration at Ottenby, Sweden, **d** number of ringed juvenile curlew sandpipers during autumn migration at Ottenby, Sweden, **e** percentage of juvenile dark-bellied brent geese at wintering sites in northwestern Europe. Dots under the time axis indicate missing data. At top we have indicated inferred periodicity of the lemming population numbers. Data and sources are given in Appendix 2

and young of waders instead of lemmings. In fact, in the time period of 1946–1995, the predation index was negatively correlated with the number of juvenile red knots (Kendall $\tau=-0.225$, $n=40$, $P<0.05$, one-tailed test) and juvenile curlew sandpipers (Kendall $\tau=-0.402$, $n=40$, $P<0.001$, one-tailed test) caught at Ottenby. This contrasts with the ringing numbers of adults, which did not show a negative correlation with the index of predation pressure (red knot: Kendall $\tau=0.100$, $n=40$, $P>0.05$; curlew sandpiper: Kendall $\tau=0.216$, $n=40$, $P>0.05$, one-tailed test). Likewise, the numbers of ringed juvenile red knots, sanderlings and curlew sandpipers passing Helgoland (Germany), and the percentage of juvenile red knots, curlew sandpipers, sanderlings, and ruddy turnstones wintering in Southern Africa, was negatively correlated with the predation index (Table 1). These find-

Table 1 Kendall rank-order correlation coefficient (τ) for reproduction records (total number of juveniles ringed and % juveniles ringed) in waders versus the inferred predation on Taimyr (cf., Appendix 2). *P*-values refer to one-tailed tests

Species	Measure	Area	<i>n</i>	Kendall- τ	<i>P</i> -level
Red knot	Number juv.	Germany	23	-0.51	<0.001
Sanderling	Number juv.	Germany	23	-0.47	<0.001
Curlew sandpiper	Number juv.	Germany	23	-0.59	<0.001
Red knot	% juv.	South Africa	15	-0.48	<0.01
Sanderling	% juv.	Southern Africa	15	-0.61	<0.001
Curlew sandpiper	% juv.	South Africa	18	-0.61	<0.001
Ruddy Turnstone	% juv.	Southern Africa	11	-0.41	<0.05

Table 2 Kendall rank-order correlation coefficient (τ) for the recorded population variables of lemmings, arctic fox, geese, and waders (cf., Appendix 2) versus the EAP climate index for the month of May, 1946–1995. Our climate impact hypothesis predicts positive correlations, therefore, *P*-values refer to one-tailed tests

Species	Measure	Area	<i>n</i>	Kendall- τ	<i>P</i> -level
Lemming	Abundance index	Taimyr	37	0.11	>0.05
Lemming	Predation index	Taimyr	36	-0.15	>0.05
Arctic fox	% occupied dens	Taimyr	36	0.22	>0.05
Brent goose	% juv./reprod. ad.	NW Europe	42	0.10	>0.05
White-fronted goose	% juv./reprod. ad.	NW Europe	45	-0.01	>0.05
Red knot	Number juv.	Ottenby	46	0.16	>0.05
Red Knot	Number juv.	Germany	23	-0.14	>0.05
Red Knot	% juv.	South Africa	15	0.19	>0.05
Curlew sandpiper	Number juv.	Ottenby	46	0.19	>0.05
Curlew sandpiper	Number juv.	Germany	23	-0.13	>0.05
Curlew sandpiper	% juv.	South Africa	18	-0.03	>0.05
Sanderling	Number juv.	Germany	23	-0.07	>0.05
Sanderling	% juv.	Southern Africa	15	0.00	>0.05
Turnstone	% juv.	Southern Africa	11	0.15	>0.05
Red knot	Number ad.	Ottenby	46	-0.01	>0.05
Red knot	Passage of ad.	Ottenby	41	0.05	>0.05
Curlew sandpiper	Number ad.	Ottenby	46	-0.04	>0.05
Curlew sandpiper	Passage of ad.	Ottenby	46	-0.05	>0.05

ings are also in agreement with the bird–lemming hypothesis.

Reproductive success in the dark-bellied brent goose (as recorded in northwestern Europe) was negatively correlated with the predation index. This is true whether reproductive success is measured as the average proportion of juveniles in wintering flocks (Kendall τ = -0.600, n = 39, P < 0.001, one-tailed test), or as the number of juveniles per estimated reproductive adult (Kendall τ = -0.559, n = 38, P < 0.001, one-tailed test). Reproduction of the white-fronted goose was also negatively correlated to the predation index, whether measured as the percentage of juveniles (Kendall τ = -0.305, n = 38, P < 0.01, one-tailed test), or as the number of juveniles per estimated reproductive adult (Kendall τ = -0.286, n = 37, P < 0.01, one-tailed test), but not as strong as in the brent goose. The inter-annual variation in reproduction (variance in juveniles per reproductive adult) is lower (0.11) in the white-fronted goose than in the brent goose (0.17; $F_{44,47}$ = 1.55, P < 0.05, one-tailed test). Furthermore, unlike the brent goose, the white-fronted goose showed no year of near-complete breeding failure (Appendix 2).

Cyclicity and climate oscillation

The fluctuations in the numbers of juvenile red knots and curlew sandpipers caught at Ottenby were tested by Fourier analysis (Fig. 3). Both species showed a significant deviation from random noise, with a maximum spectral density in the number of birds at the period length of 3 years. The median date of the annual passage of adult red knot and curlew sandpiper showed a spectral density peak at the period length of 3 years, and in the curlew sandpiper also a dominating influence of a 5–6-year periodicity. Since the latter periodicity is simply a multiple of the overall 3-year dynamics, it presumably reflects a lower success of capturing migrating curlew sandpipers in certain peak years. Fourier analysis revealed a 3-year cyclic pattern in the records of lemming abundance, and in the proportion of first-winter percentages of brent goose wintering in northwestern Europe, as well as in the fraction of juveniles of white-fronted goose in Britain and the Netherlands (Fig. 3).

The progression of spring in the breeding area, as revealed from the EAP index for May, did not correlate with any of the population variables tested in relation to the bird–lemming hypothesis (Table 2). The NAO index,

Fig. 3 Spectral analyses using Fourier transformation of different population fluctuation measures: **a** abundance index of the lemmings on Taimyr; **b** percentage of dens occupied by breeding arctic fox on western Taimyr; **c** annual ringing numbers of juvenile red knots during autumn migration at Ottenby, Sweden; **d** annual ringing numbers of juvenile curlew sandpipers during autumn migration at Ottenby, Sweden; **e** median ringing date of adult red knots during autumn migration at Ottenby, Sweden; **f** median ringing date of adult curlew sandpipers during autumn migration at Ottenby, Sweden; **g** inferred breeding success (number of juveniles per breeding adult) in the dark-bellied brent goose from winter counts in northwestern Europe; **h** inferred breeding success (number of juveniles per breeding adult) in the white-fronted goose from winter counts in Britain and the Netherlands. The D -statistic of the Kolmogorov-Smirnov test is presented, here indicating deviation from random noise. * $P < 0.05$, ** $P < 0.01$. Data and sources are given in Appendix 2

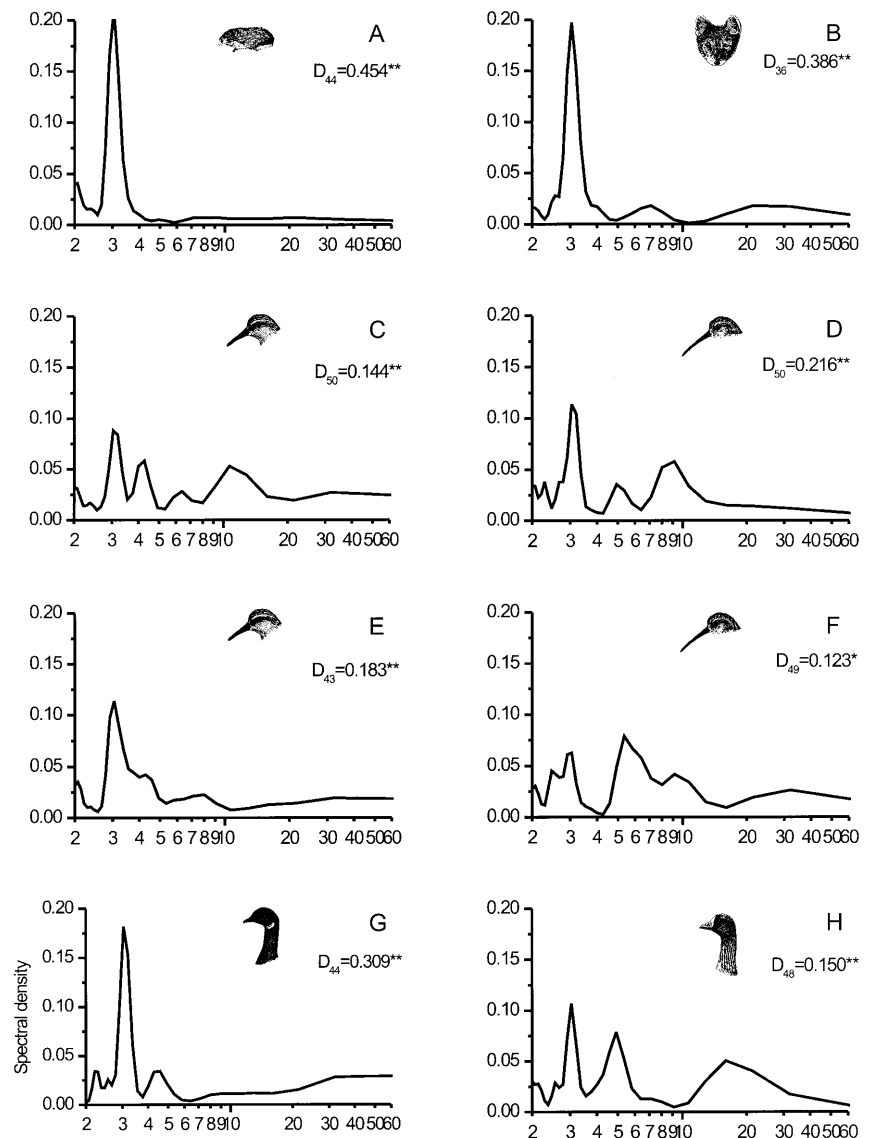


Table 3 Kendall rank-order correlation coefficient (τ) for the annual percentage of juvenile birds per reproductive adult in the dark-bellied brent goose and white-fronted goose (cf., Appendix 2) versus the NAO climate index for the months October–March, 1950–1995. Our climate impact hypothesis predicts positive correlations, therefore, P -values refer to one-tailed tests

Month	Brent goose			White-fronted goose		
	n	Kendall- τ	P -level	n	Kendall- τ	P -level
October	42	0.02	>0.05	45	-0.04	>0.05
November	42	-0.05	>0.05	45	-0.24	>0.05
December	42	0.09	>0.05	45	-0.07	>0.05
January	42	-0.06	>0.05	45	0.10	>0.05
February	42	-0.01	>0.05	45	0.08	>0.05
March	42	-0.03	>0.05	45	-0.08	>0.05

indicative of autumn and winter conditions for the geese in northwestern Europe, did not correlate positively with the proportion of recorded juvenile birds in the white-fronted goose or the brent goose (Table 3). It is worth noting that negative correlations are unrealistic, since a low proportion of juvenile birds can hardly be caused by mild weather.

Discussion

The occurrence of waders at Ottenby

The inter-specific correlations between numbers of red knot and curlew sandpiper, both adults and juveniles, stopping over at Ottenby in autumn, demonstrate the influence of common factors, either on the breeding grounds or during the southward migration. Since only the numbers of juvenile birds correlate with the preda-

tion index from Taimyr, the inter-specific correlation of juvenile red knot and curlew sandpiper is presumably related mainly to factors on the breeding grounds, whereas the correlation of adult numbers is likely caused by factors during migration, such as weather and trapping conditions.

The lack of intra-specific correlation between adult and juvenile birds might, however, be related to differences in the numerical regulation, i.e., that the number of adults depends primarily on the survival during the non-breeding season, whereas number of juveniles mainly depends on the reproductive success. Additionally, the two age groups may be exposed to different ambient conditions during migration. At Ottenby, the juveniles passed on average 22 days later than the adults in the red knot, and 33 days later in the curlew sandpiper, which is in the range of the approximately 2–4 weeks previously reported from the Baltic Sea area (Brenning 1986, 1993; Gromadzka 1987; Kube and Struwe 1994).

The relationships found between date of passage of adults at Ottenby and predation index in the red knot and the curlew sandpiper indicate that the start of the autumn migration probably depends on breeding success. In years of low predation pressure a relatively large number of pairs will breed successfully, and hence leave the breeding area after the young have become independent. This is in contrast to years of high predation pressure, when many clutches and young will be lost. The red knot usually does not attempt to lay a replacement clutch when the first clutch has been lost by predation, and on Taimyr the birds seem to disappear early in years with poor breeding success (Tomkovich and Vronsky 1988; Tomkovich et al. 1994). In the curlew sandpiper, there is no report of replacement of failed clutches. Thus, both species have a breeding system resulting in an overall earlier start of autumn migration in years of high predation pressure than in years of low predation pressure.

Further evidence from geese and waders

So far, the best support for the bird–lemming hypothesis comes from fluctuations in the reproductive success of dark-bellied brent goose (Summers and Underhill 1987; Summers et al. 1998). These fluctuations appear to be controlled primarily by biotic factors, rather than abiotic factors such as climatic oscillations (cf., Table 2, 3). The migration pattern and demographic structure of geese differ from those of waders, making demography or factors experienced during migration unlikely to cause the inter-annual co-variation in reproductive success. Therefore, the correlations found between lemming abundance and reproduction in both geese and waders (Fig. 2), suggest a common influence on the breeding grounds, rather than processes in the winter quarters. Field observations from breeding grounds on the Taimyr peninsula (Underhill et al. 1993) and the Vaygach Island, at the boundary of the Pechora and Kara seas (Syroechkovskiy et al. 1991), support the notion that predators, such as the ar-

ctic fox, switch from feeding on lemmings to eggs and young of geese and waders in the year following crashes of lemming populations.

Taken together, the combined evidence, including the present study, now provide support for co-variation in the breeding success of the dark-bellied brent goose, the Russian subspecies of white-fronted goose (Van Impe 1996), and at least four arctic breeding wader species, i.e., red knot, sanderling, curlew sandpiper, and ruddy turnstone (Roselaar 1979; Robertson 1981; Summers 1986; Summers and Underhill 1987; Summers et al. 1987b, 1989, 1998; Underhill 1987; Underhill et al. 1989; Dierschke 1994; this study). The inter-annual population fluctuations on the wintering grounds are more pronounced in the species nesting mainly in Taimyr, i.e., brent goose, red knot and curlew sandpiper, than in those with a more extended breeding range, i.e., white-fronted goose, sanderling and turnstone (cf., Appendix 2).

Periodicity pattern

Data on red knot, curlew sandpiper, brent goose, lemmings and arctic fox in 1943–1995 suggest a dominant 3-year cyclicity of breeding success in Taimyr (Fig. 3). For lemmings, a 4-year periodicity seems to have occurred in 1943–1947, and in 1963–1967 (Fig. 2). An older time series of lemming abundance for 1919–1938 from an area between the Khatanga and Lena rivers, i.e., just east of Taimyr, shows a regular 3-year periodicity, interrupted only by one 2-year period in 1922–1924 (Romanov 1941). In contrast to the constant 3-year rhythm during 1919–1922, 1924–1938, and 1967–1995, the lemming periodicity in central Siberia has varied between 2, 3 and 4 years during the periods of 1922–1924 and 1943–1967. The two lemming species on the Nearctic tundra (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) show more irregular time series than the lemming populations in Siberia (*L. sibiricus* and *D. torquatus*), with 2–6 years elapsing between peaks (Batzli et al. 1980; Finerty 1980; Pitelka and Batzli 1993).

The cause of the cyclic pattern in the abundance of lemmings is still debated, i.e., whether lemming population dynamics is top-down regulated by predators or bottom-up regulated by plant chemical defense. Seldal et al. (1994) showed that foraging by lemmings on plants induces the production of proteinase (trypsin) inhibitors in the plant. Such inhibitors (chemical defense compounds) reduce the digestion efficiency of proteins in the intestinal lumen of microtines, leading to impaired health, reflected by enlarged pancreas and spleen, which in turn may lead to declining population numbers (Seldal et al. 1994). In support of this hypothesis, the shape of the peaks of lemming abundance curves in Fennoscandia indicate that lemming cycles are generated as a result of the lemmings interacting with their food plants, rather than with their predators (Turchin et al. 2000).

Indirect effects

The populations of red knot and curlew sandpipers breeding in Siberia are roughly 350,000 and 1.1 million birds, respectively (Piersma and Davidson 1992; Rose and Scott 1994). These birds are known to consume considerable amounts of benthic invertebrates. For instance, in the Berg River estuary, South Africa, curlew sandpipers alone consume up to 38% of the annual production of nereid worms (Kalejta 1992), and in three months remove 77% of the initial (January) standing biomass of these polychaetes (Kalejta 1993). In a study at the Banc d'Arguin, Mauritania, the red knot was found to remove many small prey items (Zwarts et al. 1990). In wintering (and summering) areas with large numbers of red knots and curlew sandpipers, such as in Mauritania (Trotignon et al. 1980; van Dijk et al. 1990; Zwarts et al. 1998a, b), Southern Africa (Summers et al. 1987a; Underhill 1997a, b) and Australia/New Zealand (Sagar 1986; Lane 1987; Barter 1992), these sandpipers

may have a significant impact on the littoral benthos. Thus, the cyclicity in numbers of lemmings results in periodically varying numbers of waders migrating south, with subsequent variations in the predation pressure on littoral invertebrates in Africa (Robertson 1981; Underhill et al. 1989; Summers et al. 1998), Australia (Lane 1987), Tasmania (Thomas 1970) and New Zealand (Falla et al. 1981). Hence, the multi-annual fluctuations in population numbers of arctic lemmings might not only affect the northern tundra ecosystem, but may even have far-reaching, cross-system repercussions in the Southern Hemisphere.

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Appendix 1

The annual number ringed, and median ringing date of red knot *Calidris canutus* and curlew sandpiper *C. ferruginea* at Ottenby

Year	Red knot				Curlew sandpiper			
	Adults		Juveniles		Adults		Juveniles	
	<i>n</i>	Median	<i>n</i>	Median	<i>n</i>	Median	<i>n</i>	Median
1946	0	–	0	–	0	–	97	06 Sep
1947	0	–	0	–	11	01 Aug	0	–
1948	24	26 Aug	35	27 Aug	11	05 Aug	13	30 Aug
1949	119	05 Aug	1	17 Aug	135	03 Aug	33	25 Aug
1950	31	28 Jul	3	10 Sep	36	02 Aug	17	19 Sep
1951	4	22 Jul	4	28 Sep	25	21 Jul	22	08 Sep
1952	15	17 Aug	5	17 Aug	29	26 Jul	7	30 Aug
1953	159	03 Aug	87	30 Aug	94	29 Jul	235	31 Aug
1954	25	31 Jul	22	02 Sep	70	21 Jul	105	19 Aug
1955	0	–	0	–	1	24 Aug	2	23 Aug
1956	26	10 Aug	32	19 Sep	24	30 Jul	55	21 Aug
1957	10	26 Aug	67	31 Aug	11	26 Jul	1	17 Aug
1958	51	05 Aug	0	–	23	29 Jul	2	26 Aug
1959	0	–	28	27 Aug	9	17 Jul	40	30 Aug
1960	1	19 Aug	12	23 Aug	6	24 Jul	62	23 Aug
1961	2	12 Aug	0	–	33	15 Aug	6	03 Sep
1962	5	27 Jul	3	20 Aug	39	03 Aug	3	05 Sep
1963	15	12 Aug	10	19 Aug	38	12 Aug	150	18 Aug
1964	4	02 Aug	0	–	17	22 Jul	44	09 Sep
1965	69	07 Aug	3	08 Sep	41	09 Aug	18	08 Sep
1966	68	11 Sep	128	16 Sep	16	12 Aug	24	13 Sep
1967	4	12 Aug	15	31 Aug	7	12 Aug	54	06 Sep
1968	0	–	0	–	1	03 Aug	0	–
1969	5	27 Aug	90	27 Aug	7	18 Jul	257	26 Aug
1970	22	02 Aug	100	08 Sep	5	03 Aug	63	29 Aug
1971	10	17 Aug	0	–	71	24 Jul	4	21 Aug
1972	11	25 Aug	48	25 Aug	6	06 Aug	197	27 Aug
1973	6	24 Aug	21	26 Aug	5	14 Aug	10	03 Sep
1974	93	29 Jul	0	–	63	29 Jul	0	–
1975	1	09 Sep	10	05 Sep	35	25 Jul	56	27 Aug
1976	70	01 Aug	25	12 Sep	4	09 Aug	46	05 Sep
1977	77	22 Jul	1	19 Oct	59	23 Jul	4	11 Sep

Appendix 1 (continued)

Year	Red knot				Curlew sandpiper			
	Adults		Juveniles		Adults		Juveniles	
	<i>n</i>	Median	<i>n</i>	Median	<i>n</i>	Median	<i>n</i>	Median
1978	20	25 Aug	144	27 Aug	66	19 Jul	213	26 Aug
1979	10	29 Aug	34	30 Aug	14	22 Jul	63	01 Sep
1980	83	19 Jul	1	08 Aug	72	21 Jul	36	28 Aug
1981	37	01 Aug	2	17 Aug	41	23 Jul	32	20 Aug
1982	22	23 Aug	6	25 Aug	34	18 Aug	19	19 Aug
1983	7	04 Aug	4	04 Sep	58	22 Jul	3	16 Sep
1984	0	–	0	–	37	24 Jul	3	12 Sep
1985	13	24 Jul	13	09 Sep	8	29 Jul	28	29 Aug
1986	3	03 Aug	1	11 Aug	34	20 Jul	11	22 Aug
1987	13	07 Aug	1	02 Sep	21	03 Aug	27	06 Sep
1988	58	03 Aug	21	18 Sep	14	06 Aug	151	24 Aug
1989	107	06 Aug	9	07 Sep	38	21 Jul	1	28 Oct
1990	11	20 Aug	42	24 Aug	57	18 Jul	135	31 Aug
1991	5	18 Jul	1	25 Aug	33	16 Jul	13	24 Aug
1992	293	02 Aug	8	03 Sep	74	02 Aug	12	02 Sep
1993	54	09 Aug	12	21 Aug	148	25 Jul	17	16 Aug
1994	0	–	8	10 Sep	14	03 Aug	90	04 Sep
1995	31	23 Jul	1	21 Aug	18	25 Jul	9	02 Sep

Appendix 2

Tabulated data on lemming abundance, arctic fox
Alopex lagopus abundance, and measurements of reproductive
 success in birds

The lemming abundance is presented by two data sets, and their rounded average, from which a predation index is calculated (see under Methods). The abundance of arctic fox is presented as the percentage of dens occupied by breeding animals. The data of dark-bellied brent goose *Branta b. bernicla* reproduction are compiled winter records from northwestern Europe, and winter counts of the white-fronted goose *Anser a. albifrons* are from Britain and the Netherlands. Geese data are presented as the percentage of juveniles in winter flocks, and also as number of juveniles per reproductive adult (Ebbinge 1989). When several independent counts have been found in the literature, the average has been calculated. The measurements of reproduction in the waders, red knot *Calidris canutus*, curlew sandpiper *C. ferruginea*, sanderling *C. alba*, and ruddy turnstone *Arenaria interpres*, are presented as number of juveniles at stopover sites (Ottenby and Helgoland), and as percentage of total numbers in wintering flocks in Southern Africa.

The indices in the column titles indicate source of data as follows: 1 1943–1950: Sdobnikov (1957); 1969–1986: Underhill (1987), Underhill et al. (1989); 1983: Pienkowski (1983); 1984–1993: Rykhlikova and Popov (1995); 1988: Tomkovich (1989); 1989: Prokosch and Hotker (1990), Kondratyev (1992); 1990: Yésou (1991), Yuvlov (1993); 1991: Underhill et al. (1993), Ryabitsev (1993), Schekkerman and van Roomen (1995); 1992: Spiekman and Groen (1993), Tomkovich (1994a), Underhill et al. (1993); 1993: van Dijk and Venema (1993), Tomkovich (1994b); 1994: Tomkovich and Lebedeva (1996), Angerbjörn et al. (1999); 1995: P. Tomkovich personal communication. 2 From typical tundra on western Taimyr, Kokorev and Kuksov (2002). 3 From typical tundra on western Taimyr Kokorev and Kuksov (2002). 4 1954, 1956–1975: Ogilvie and St Joseph (1976); 1955: Burton (1958); 1970–1986: Ebbinge (1989); 1976–1984: Summers and Underhill (1987); 1985:

Ebbinge (1989); 1986: Salmon (1986); 1987: Salmon (1987); 1987–1991: Ebbinge and Spaans (1995); 1988: Salmon (1988); 1989: Salmon (1989); 1990–1991: Kirby (1991, 1992); 1992: Cranswick (1993); 1993–1995: Mitchell and King (1994, 1995, 1996). 5 Lebreton (1948); Boyd (1965); Ogilvie (1978); Van Impe (1996). 6 Dierschke (1994, V. Dierschke personal communication. 7 Underhill et al. (1989). 8 Underhill (1987). 9 Summers et al. (1987b). 10 Summers et al. (1989)

Appendix 2 (continued)

Year	Lemmings		Arctic fox		Brent goose		White-fronted goose		Red knot		Curlew sandpiper		Sanderling		Ruddy turnstone	
	Taimyr		Taimyr		northwestern Europe		Britain and the Netherlands		Ottenby		Helgo-land		Helgo-land		S. Africa	
	Abundance ¹	Abundance ²	Predation index ³	% occupied dens ³	% juv. ⁴	Juv. per . ⁵	% juv. ⁵	Juv. per . ⁶	No. juv.	% juv. ⁶	No. juv.	% juv. ⁶	No. juv. ⁶	% juv. ⁶	% juv. ⁹	% juv. ¹⁰
1985	3	3	0.5	35	35	0.54	45.0	1.06	13	567	25	58	427	30		
1986	1	0	2.5	16	0.1	0.00	17.0	0.37	1	25	0	1	112	0		0
1987	0	0	2	0	1.6	0.02	26.0	0.42	1	97	11		287			
1988	3	2.25	3	20	34.4	0.53	40.0	0.90	21	71	227		155			
1989	0	0	3	0	1	0.02	23.0	0.50	9	34	0		340			
1990	1	1.5	1	6	21.4	0.28	32.0	0.61	42	177	234		412			
1991	3	2.25	3	33	31.2	0.58	41.0	1.02	1	305	59		379			
1992	1	0	2	15	0.1	0.00	12.0	0.23	8	32	2		65			
1993	1	0.75	1	15	18	0.22	28.0	0.44	12	106	30		106			
1994	3	1.5	2	25	5.8	0.08	21.0	0.37	8	99	20		301			
1995	1	0	2	0	0.3	0.00			1		9					

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