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Boyd, H.; Piersma, T.

Published in:
Ardea

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2001

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Boyd, H., & Piersma, T. (2001). Changing balance between survival and recruitment explains population trends in Red Knots Calidris canutus islandica wintering in Britain, 1969-1995. *Ardea*, *89*(2), 301-317.

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CHANGING BALANCE BETWEEN SURVIVAL AND RECRUITMENT EXPLAINS POPULATION TRENDS IN RED KNOTS *CALIDRIS CANUTUS ISLANDICA* WINTERING IN BRITAIN, 1969-1995

HUGH BOYD[1] & THEUNIS PIERSMA[2,3,*]

Boyd H. & T. Piersma 2001. Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus islandica* wintering in Britain, 1969-1995. Ardea 89(2): 301-317.

The demography of Red Knots *Calidris canutus islandica* wintering in Britain from 1969 to 1995 was examined using published data on winter numbers, unpublished ringing data, and information on the percentages first year birds in late autumn and winter (defined here as 'recruitment'). The maximum time between ringing and reporting was 24 years for a Red Knot ringed as an adult. The mortality rate of juveniles during their first winter was four times that of adults, but did not differ later. For three periods, recruitment minus mortality corresponded qualitatively with changes in population size. In 1969-77, when the numbers wintering in Britain were declining by 8.7% annually, the mean percentage juveniles in the wintering population was estimated at 12.1% and the mean adult mortality rate was estimated at 23.6% per year (balance -11.5%). In 1977-85, when numbers were increasing by 4.6% per annum, the average juvenile percentage was high (28.8%), but the adult mortality rate was lower than in the previous period (19.6%; balance +9.2%). In 1985-95, when wintering numbers showed no clear trend (average +0.9% per annum) but were still below those in 1969-72, juvenile percentages were again quite low (mean of 13.8%), but the adult mortality rate was also low (14.2%; balance -0.4%). Cold summers reduced both recruitment and adult survival. British Knot populations appear to fluctuate as a consequence of factors affecting survival as well as reproduction. There is evidence for density-dependent processes that affect overall reproductive success. Although probably acting sometime from late winter to early autumn, the mechanisms causing such density-dependence remain mysterious.

Key words: *Calidris canutus islandica* - demography - population dynamics - density-dependence - counts - ringing - survival - weather - arctic

[1]National Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, Ottawa K1A 0H3, Canada; [2]Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; [3]Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 45, 9750 AA Haren, The Netherlands; *Corresponding author; E-mail: theunis@nioz.nl

INTRODUCTION

Rates of survival and recruitment are necessary components of models that describe and explore the causes of changes in the size of bird populations (Newton 1998). Considering the intense world-wide research efforts on long-distance migrating waders in recent years, it is remarkable that so few estimates of survival and recruitment have become available for this group of birds (Evans 1991; but see Peach *et al.* 1994; Marks & Redmond 1996; Hitchcock & Gratto-Trevor 1997 for notable exceptions). Indeed, demographic studies are presently available for only 30% of the world's plover and sandpiper species (Piersma *et al.* 1997). Though the Red Knot *Calidris canutus* (henceforth simply called Knot) is one of the most intensively studied birds breeding in the High Arctic (Piersma & Davidson 1992), until recently the only published estimate of its annual adult survival rate was one of 0.676, based on less than a hundred recoveries of Knots ringed in Scandinavia before 1955 (Boyd 1962). Since that time much larger numbers have been ringed in western Europe, especially in the United Kingdom, where about 3/4 of the population of *C. c. islandica* spends the winter (Smit & Piersma 1989). *Islandica* Knots are presently the most numerous of the five or six extant subspecies of Knots (Piersma & Davidson 1992; Piersma & Baker 2000).

The first purpose of this contribution is to enlarge on brief treatments of annual survival in Piersma (1994) and Atkinson (2000; see also Atkinson *et al.* 2000), as both analyses suggested that recent survival rates were higher than the pre-1955 estimate. For relatively long-lived birds such as Knots, one would predict (Hitchcock & Gratto-Trevor 1997; Piersma & Baker 2000), that changes in population size would mainly be due to variation in adult survival (which is expected to be very constant), rather than recruitment (which is likely to be quite variable). Our second aim is therefore to examine the relative importance of these two factors in determining the numbers of Knots wintering in Britain, as assessed by the winter index developed by Underhill & Prys-Jones (1994). This index showed a decline from 1969 to 1977 and then an increase until about 1985. From 1985-95 numbers showed no sustained trend. Prater (1976, 1981) identified the Knot as the only wader species which, during the period 1969-70 to 1976-77, had decreased markedly in Britain and France. Note that since 1995 there was again a substantial decrease (Pollitt *et al.* 2000).

Over the three time intervals between 1969 and 1995 recruitment of young birds in the population could be estimated on the basis of percentages of juveniles recorded in Knot catches on the Wash and elsewhere in Britain. We explore briefly whether the population dynamic variables are correlated with average air temperatures in the breeding and nonbreeding areas, or with an index of predation risk on the tundra breeding grounds.

MATERIALS AND METHODS

Changes in population size of Knots wintering in Britain were based on the published midwinter counts expressed as the winter index developed by Underhill & Prys-Jones (1994; see also Prys-Jones *et al.* 1994, supplemented by Cranswick *et al.* 1995). These published data on population changes led us to estimate the mean annual survival rates during four sub-periods in 1960-95: one (1960-68) for which the population size and trend are unknown, and three (1969-77,1977-85 and 1985-95) with known trends (Appendix 1). In the period 1969-77, the average change in winter index from one winter to the next was -8.7% (computed from between-winter changes including the data point for the 1976-77 winter). Over the period 1977-85 the winter index showed an average increase of 4.6% (this again includes changes till the data point for 1984-85). From 1985-95 the population was more or less stable with on average a small increase of 0.9% per year.

Rings, recoveries and controls

Few Knots were ringed in Britain until the early 1960s. The first large catches were made in 1963 by the Wash Wader Ringing Group (WWRG), using the Wildfowl Trust's rocket-nets. Ringing groups in other parts of the country soon began to emulate the WWRG's use of cannon- and flight-nets to catch waders. By the end of 1995, 87,786 Knots had been ringed in Britain and had produced 812 recoveries of dead birds. Many more British-ringed Knots had been recaptured and released alive (*n* = 1233), chiefly on British estuaries, but also by ringers in Iceland, The Netherlands, Germany and Norway. Though ringing groups presumably kept records of all these controls, including repeats (i.e. those taken again in the same season at, or close to, the site where they were first ringed), the central ringing files kept by the British Trust for Ornithology (BTO) exclude recaptures by the same ringing group within 30 km of the marking site (Mead *et al.* 1995).

Based on the reviews by Davidson & Wilson (1992) and Piersma *et al.* (1992) and the analysis of Boyd & Piersma (2001), we used a simple classification system to select the data-points indicating the *islandica* subspecies. Birds caught in Britain in winter (October-April) should be *islandica*, while those taken in May and July-September might be either *islandica* or the Siberian-breeding subspecies *canutus* that winters in West-Africa (Piersma *et al.* 1992). For birds caught in these periods some are recovered or controlled at a time and a place appropriate for the subspecies *islandica* (Boyd & Piersma 2001). Because of the preponderance of recovery records and controls in Britain, only these have been used for estimating survival. Most recoveries elsewhere, particularly those in Greenland and north-east Canada, where dead birds are unlikely to be found and reported to the BTO with the same probability as in Britain, have been concentrated in a few years (see below). Although they indicate that substantial losses sometimes occur in the summer months, these recoveries, and those from continental Europe, have not been used in estimating annual survival.

Estimating survival of ringed birds

The primary survival analysis is for birds ringed as first-winter and older birds combined and is based on 392 recoveries and 828 controls (see Appendix 2) in Britain *after* the calendar year in which they were marked. There are many methods of estimating survival from recoveries and recaptures of marked animals (Ricker 1975; Seber 1982; Brownie *et al.* 1985). The most sophisticated stochastic models, which allow for annual variations in reporting rates as well as in survival, require large recovery samples if they are to yield precise and accurate estimates. The annual and cumulative recovery-rates of British-ringed Knots were low in the early years of ringing and have decreased even further (see below). Estimates of annual survival and recovery rates based on these small annual samples have wide confidence limits.

The statistical methods used here are applications of stochastic maximum likelihood models devised by Haldane (1953, 1955), Jolly (1965) and Seber (1970, 1982). Haldane's method (Model 3 of Brownie *et al.* 1985) is a modification of Lack's method (Lack 1943), to allow for the survival of some birds beyond the end of the study period. It assumes that survival of adults does not vary with age and that the annual survival rate (s) and the recovery rate were constant during all the years included in the sample period. This method does not require knowledge of the numbers of birds released in any year, and is still valid if recoveries in an initial period after marking are set aside. We know that in the present study the assumption of constant rates is not valid because the cumulative recovery rate has been declining. Breaking the entire 36-year period into four, as we have done, offsets this weakness, as the variation in any subperiod is relatively small.

The Jolly-Seber model (Model 0 of Brownie *et al.* 1985), which also assumes that the rate parameters are age-independent, allows the survival and recovery rates to be year-specific, except that the recovery and reporting rates in the year of marking are not expected to be the same as in subsequent years. This model, which uses the numbers of birds marked each year, is more general than Haldane's. The methods of estimating standard deviations are those described by Seber (1982).

The sex of Knots can only be established reliably by using a molecular probe (Baker *et al.* 1999), a technique developed very recently. Consequently, it is not yet possible to look for differences in the survival rates of females and males (cf. Nebel *et al.* 2000).

Ringing of Knots in Britain has occurred in all months except June and July, but (except for WWRG catches) the numbers ringed in different months are not readily available. We have therefore used the Jolly-Seber model only on the total annual catches. Initially, we used Haldane's method to estimate separately the survival of Knots ringed in October-April (i.e. almost entirely *islandica*) and those ringed in August/September, setting aside recoveries in the year of marking and using only those in subsequent calendar years, following the example of Haldane (1955) and many other workers on non-game birds. As the estimates from ringing in early autumn and in winter proved to be very similar, we have combined them. The records of controls are incomplete, because of the censoring noted earlier. Treating them as equivalent to recoveries, we produced a second set of survival estimates, which differed surprisingly little from those based on recoveries. To maximise the numbers available, we therefore combined the series from recoveries and from controls to produce the estimates presented here.

Estimating recruitment

The WWRG catch records provide the longest-running index of annual variations in the numbers of juveniles reaching Britain in the years 1960-98. Here, only the records from 1969-95 are used, to be comparable with the winter index data. First year birds continue to be recognisable throughout the winter (Prater *et al.* 1977). There are within-season variations in the WWRG samples, which are spread across the period from mid-August (when juveniles begin to arrive) to the following April. In particular, the proportion of juveniles is nearly always higher in small catches than in large ones (Table 1), perhaps because juveniles are more likely than adults to roost and feed away from the large groups. We omitted catches in early August, as few juveniles arrive on the non-breeding areas before 20 August. We also discarded a few WWRG catches in which a large fraction of the catch could not be identified as 'juveniles' or 'adults' (all those more than a year old).

To obtain the largest possible samples, we have combined all fully age-classified catches in the period 16 August-30 April. For the years 1971-86 a second data set (Underhill *et al.* 1989) was available. There were substantial discrepancies between the WWRG values and those reported by Underhill *et al.* (1989) in six of the eleven years in which direct comparisons were possible. In 1978-86, the percentages of young in the two sets were similar (averages of 31.5% and 29.4%, respectively). They had been quite different in 1971-76, a period of low recruitment (16.6% and 7.4%). Although the Underhill data included some WWRG individuals, we combined the two series in a pooled estimate, weighted by sample size (Appendix 1). This index of 'recruitment' is of birds that have not only fledged but that also completed migration to Britain. The index thus reflects chick production and losses on the breeding grounds as well as during southward migration. When testing for correlates of variations in production, we used arcsin transformations of the percentages of young.

Estimating survival from the winter index

If the percentages of first year birds in the catches can be taken as representative of the entire stock, they can be applied to the winter index to

Table 1. Numbers of juvenile and adult Knots taken by the WWRG in large (> 100 Knots) and smaller catches, 1960-95.

Time of year	Large catches				Small catches			
	juvenile	adult	total	% juv.	juvenile	adult	total	% juv.
Aug. / Sep.	3615	11 440	15 055	24.0	881	820	1701	51.8
Oct. / Apr.	2173	19 643	21 816	10.0	784	3414	4198	18.7
Total	5788	31 083	36 871	15.7	1665	4234	5899	28.2

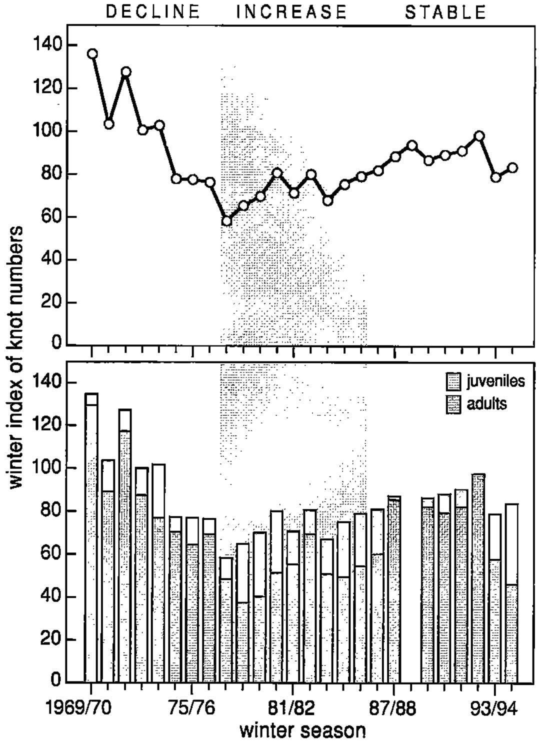

Fig. 1. The UK winter index of Knots numbers from 1969-70 through 1994-95 (Prys-Jones *et al.* 1994; Cranswick *et al.* 1995) (top) and partitioned into adults and juveniles by application of the percentage of young in catches in Britain (see Appendix 1) (bottom). The three distinct periods of population change, used throughout this study, are indicated.

estimate the relative numbers of adults and juveniles in the British wintering population by multiplying the UK winter index (Appendix 1) by the proportion of juveniles in the assembled ringing catches (Fig. 1). *Islandica* Knots winter in parts of the British Isles not covered by the midwinter counts, and also in the Wadden Sea and France. If most adult Knots return to wintering areas they have used previously and if most juveniles winter where their parents do (although they likely migrate without parental guidance), so that the British population can be treated as nearly 'closed', annual survival can be estimated from the winter index, using the equation:

$$S(\mathrm{t}) = A(\mathrm{t}+1)/\,T(\mathrm{t})$$

in which S = survival from one winter to the next, A(t+1) the index number of adults in year t+1 and T(t) = index number in year t. This assumes that, as noted earlier, juveniles survive as well as older birds after their first winter.

Seasonal temperatures

For summer conditions we have used monthly mean temperatures in June-August from three stations (Alert, Eureka and Resolute) in the Queen Elizabeth Islands, Nunavut, Canada, which include most of the breeding range of *islandica* (Godfrey 1992; Davidson & Wilson 1992). The data were collected and published by the Atmospheric Environment Service, Environment Canada, in the monthly series now called *Canadian Climate Summary*. Comparing this series with incomplete station records from northwest Greenland, we found no important discrepancies. The breeding range in east Greenland is represented by temperatures at Danmarkshavn (76.8°N, 18.8°W). We were only able to access data for the years 1980-96 from *Climate Monitor*. In most climatic studies summer temperatures are expressed as the mean of the daily mean air temperatures in the three months June, July and August. We have treated June and July-August separately; these periods correspond roughly to the nesting and brood-rearing periods, respectively.

For British winter weather we have used a standard source, the daily and monthly mean temperatures in central England, first compiled by Manley (1953), revised by Parker *et al.* (1992) and updated to 1996 in Hulme & Barrow (1997).

Summer predators

The breeding range of *islandica* extends from about 20°W to 110°W, and from 73°N to 83°N. There are likely to be substantial differences in the abundance of predators across that wide range, within as well as between seasons. The principal predators are gulls, skuas and Arctic Foxes *Alopex lagopus*. The only extensive quantitative data on predator numbers available are records of winter-trapped Arctic Foxes. Records of pelt exports have been kept by the Government of the Northwest Territories for many years, as this was one of the few sources of outside income for northern people. The industry collapsed in the late 1980s.

Arctic Foxes are trapped in winter. The numbers of fox pelts exported from the Inuit settlements of Grise Fiord (76.35°N, 83.14°W), on the south coast of Ellesmere Island and Resolute Bay (74.41°N, 94.50°W) on Cornwallis Island, both in the range of *islandica*, should serve as an index of fox abundance and breeding success in the preceding summer and of numbers in the following summer. From 1954 to 1988, the exports of pelts from these two settlements varied from 1353 in 1959 to only 33 in 1987. There are no records for 1962, 1966, 1980 and 1981, nor after 1988. The numbers of pelts from the two settlements are highly correlated [$r_{25} = 0.707$, $P < 0.001$]. Trapping effort is likely to have been affected by the expected ratio of revenues to costs. Prices fluctuated widely, falling in the 1980s. We therefore calculated a hypothetical second series on the assumption that prices had remained in constant 1971 dollars. This yielded estimates that were lower around 1960 and much higher for most of the 1980s. However, the unadjusted series is used here, as the differences between the two were not great enough to affect the inferences from the analyses. In testing for possible effects of fox abundance on production of young we used natural logarithms of the numbers of foxes and Knots.

RESULTS

Survival rates

A total of 77 birds were recovered or controlled in Britain more than 14 years after being ringed: 15 after 15 years, 17 after 16, 11 after 17, 12 after 18, 4 after 19, 3 after 20, 9 after 21, 3 after 22, 2 after 23 and one after 24 years, the maximum time yet recorded. That bird, ringed on the Wash as an adult on 27 August 1968, was controlled there on 1 September 1992, when it had a minimum age of 25 years.

The number of juvenile *islandica* ringed and recovered in Britain within one year of marking is rather small (50 of 405, 12.3%). Combining the numbers of first-year and adult birds caught on the Wash in August-October and the resulting number of recoveries within half a year after ringing, it is possible to estimate the relative mortality of the two age-categories over the winter. We have excluded birds ringed in August-September 1963, when there was a large influx of juveniles from the Siberian breeding grounds that yielded a considerable number of African recoveries within a few months (Boyd & Piersma 2001). There seem to have been no comparably-large influxes of juvenile *canutus* since. The ratio of the percentage of first-year birds ringed (13.4%, $n = 22,750$) and recovered within half a year (54.2%, $n = 24$) indicates that young Knots are four times (54.2/13.4 = 4.04) as likely to die during their first winter as in later winters.

Table 2 summarises both the Haldane and the Jolly-Seber estimates of mean annual survival of adults in each of four periods, three of them corresponding to periods with particular trends in the winter index. The Haldane estimates, based on the assumption that survival and reporting rates during each period are fixed, in three of the four periods are higher than the Jolly-Seber estimates, using whole year ringing and assuming annual variability in both rates.

A constant survival series compiled for the first two periods (1960-76), on the assumption that very few of these marked birds were still alive in 1995, yielded a mean annual survival rate of 0.797 (SD = 0.205). When the successive entries in that series were compared with the observed sequence of recoveries in calendar years 1,2,3,..*n* after marking, using the procedure suggested by Haldane (1955), the fit was reasonably close ($\chi^2_{22} = 22.247$, $P > 0.30$), implying that departures from the mean rate in particular years must largely have cancelled each other out and confirming that there was little variation in annual survival with age.

Table 2. Estimates of mean annual survival (*s*) of adult Knots in different periods between 1960 and 1995: from British recoveries and controls of British-ringed Knots by (A) Haldane's method and (B) the Jolly-Seber method; and from the UK winter index and percent juveniles in ringing catches calculated as the average of the yearly values (C). Below the numbers of recoveries and controls, the numbers in parentheses show the respective percentages of those newly ringed.

	1960-68	1969-77	1977-85	1985-95	1960-95
Trend in winter index	Unknown	Decrease	Increase	No change	
Numbers newly ringed	5533	42 191	15 122	21 179	78 492
Numbers of recoveries	33	143	57	52	285
(%)	(0.60)	(0.34)	(0.38)	(0.24)	(0.36)
Numbers of controls	77	358	68	97	600
(%)	(1.39)	(0.85)	(0.45)	(0.46)	(0.76)
(A) Haldane					
Mean adult *s*	0.821	0.764	0.804	0.858	0.790
SD	0.178	0.003	0.012	0.008	0.008
(B) Jolly-Seber					
Mean adult *s*	0.614	0.698	0.870	0.720	0.743
SD	0.078	0.021	0.025	0.050	0.013
(C) Winter index					
Mean adult *s*	Not known	0.776	0.754	0.807	0.791
SD		0.179	0.141	0.196	0.174

Using the percentage of juveniles in catches to partition the winter index into estimates of the relative numbers of adults and young wintering in Britain, Figure 1 shows that in most winters the estimated number of adults was far larger than that of first year birds. Table 2 compares the estimates of mean annual adult survival between 1969 and 1995 from recoveries and controls of British-ringed birds (rows A and B) and from the variations in the winter index and proportions of young by averaging the estimates for individual years within the period (row C). The overall estimate from ringed birds using the Haldane method is similar to the one based on winter index and percentage juveniles ($s = 0.79$). In the last two periods, when population size increased or was stable, the Haldane estimates are 5% higher than the survival rates based on the winter index.

Causes of death

Boyd (1962) noted that 79% of adults and 86% of juvenile recoveries from Scandinavian ringing reported before 1955 were of birds killed by man. What proportion of those recoveries may have been in Britain is not known. Some of the recovery records in the BTO files include additional information on the apparent cause of death, though in nearly 300 cases there is none. Omitting records of birds found long dead, or of rings only, 26 (6.9%) of 378 recoveries in Britain were of Knots shot, or found shot, compared with 31 (8.2%) attributed to predators. The shooting of Knots in Britain has been illegal throughout the period in which ringing has occurred. The proportion reported shot was higher before 1978 (21/185 = 11.4%) than since (5/193 = 2.6%, $\chi^2_1 = 11.60$, $P < 0.001$).

In 1961-95 the mean winter temperature in central England was 4.1°C (SD = 1.4). There were notably cold winters in 1962-63 (mean -0.3°C, second only to -1.2°C in 1683-84 since records began in 1659), 1979-80 (mean 1.6°C) and 1981-82 (2.6°C). Many waders died on the Wash and other English estuaries in 1962-63 (Boyd 1964). Among 603 birds found dead on the Wash from 26 February to 3 March 1963, 104 Knots were second only to 144 Redshanks *Tringa totanus* (Pilcher 1964). Few Knots had been ringed by 1962, so recoveries gave no additional information. No heavy losses were reported in 1979-80 and 1981-82, and in neither winter were recoveries unusually numerous.

The highest mean winter temperatures in central England after 1960 were 6.4°C in 1974-75, 6.5°C in 1988-89 and 6.2°C in 1989-90 (i.e. two in succession) and 5.9°C in 1994-95. These did not lead to markedly increased wintering numbers. The reduction in numbers in 1974-75 was probably due to heavy adult losses and low breeding success in the cold summer of 1974 (Boyd 1992). Over the entire period 1969-95 the numbers of adults and juveniles estimated to be wintering in Britain were not related statistically to temperatures in the same winter, nor to those in the preceding winter. Interestingly, however, the first-year recovery rates of Knots ringed before, or during, a warm winter were lower than for those ringed in other years: in warm winters 16 of 13,772 newly-ringed (1.16‰); in cold winters 48/17,648 (2.72‰); and in moderate winters 123/55,375 (2.22‰) ($\chi^2_2 = 9.009, P < 0.025$).

Effects of summer temperatures and Arctic Foxes

We were unable to find statistically significant correlation's between June or July-August temperatures in the Queen Elizabeth Islands or east Greenland and the percentages of young, the value of the winter index, or the change in the winter index from the previous year. There were no statistically significant correlation's between fox-pelt exports from the Queen Elizabeth Islands and temperatures in the previous summer, but the winter index for Knots was lower after winters when many Arctic Foxes were trapped on Ellesmere and Cornwallis Islands ($r_{18} = -0.383, P = 0.1$). The correlation coefficient r increased to -0.523 ($P < 0.05$) after partialling out time trends in the two series.

The springs and summers of 1972 and 1974 were exceptionally cold in north-west Greenland, on Baffin Island and across the Queen Elizabeth Islands, so that few waders bred successfully (Morrison 1977; Boyd 1992). The total of 117 recoveries from Greenland forms nearly one-sixth of all the recoveries of British-ringed Knots. About half were reported shot in staging areas on the west coast, south of 73°N. The others were taken in the Thule district, north of 75°N, where they could have been either potential breeders or passage migrants. Eighty-seven (or 74%) of the Greenland-recoveries were in 1972 and 1974, most of which (74) were in June and July. Some of the Knots shot in west Greenland and near Thule in those years, were taken because they were seen to be ringed (P. Lyngs pers. comm.). The proportions of all Greenland recoveries in the Thule district were similar in 1972 (61.8%) and 1974 (61.4%), compared with only 7.1% in other years. In 1972, cold throughout the summer, two-thirds of those northern recoveries were found before much nesting would have begun in 'normal' springs, with one-third during the breeding period, the latter in much the same proportion as in all other years. In 1974, when June was very cold, but July and August were warmer than usual, 28/35 (80%) of the north Greenland recoveries were during the period when Knots should have been nesting. The relative scarcity of recoveries in August and September in 1972 and 1974 ($n = 2$ out of 89 in total) compared to a ratio of 5/30 in all other years, seems to confirm that substantial adult losses had occurred earlier in those summers ($\chi^2_1 = 6.623, P < 0.02$).

If total adult losses were large and breeding success was very low in the summers of 1972 and 1974, the numbers of Knots wintering in Britain should have been depressed in the following winters; and they were. The winter index fell from 127 in 1971-72 to 100 in 1972-73; and from 102 in 1973-74 to 78 in 1974-75, reductions by 21% and 24% respectively. Nevertheless, reductions of similar magnitude occurred three more times: -24% from 1969-70 to 1970-71, -24% from 1976-77 to 1977-78 and -19% from 1992-93 to 1993-94.

Correlations between percentage juveniles and winter numbers

The percentage of juveniles was low after and during winters in which the index of population size was high (Fig. 2A, B). In years when winter index numbers were larger than 80-85, the percentage juveniles tended to be low. Surprisingly, the strength of the negative association between the arcsin-transformed juvenile percentage and the winter index does not depend on whether the concurrent winter index is used (Fig, 2A; r_{25} = -0.50, P = 0.011) or whether the index for the previous winter is used (Fig. 2B; r_{24} = - 0.49, P = 0.015). Yet, the somewhat tighter relationship between the percentage juveniles and the winter index in Fig. 2B compared with Fig. 2A, might indicate that winter numbers exert negative effect on recruitment especially in the upcoming breeding season.

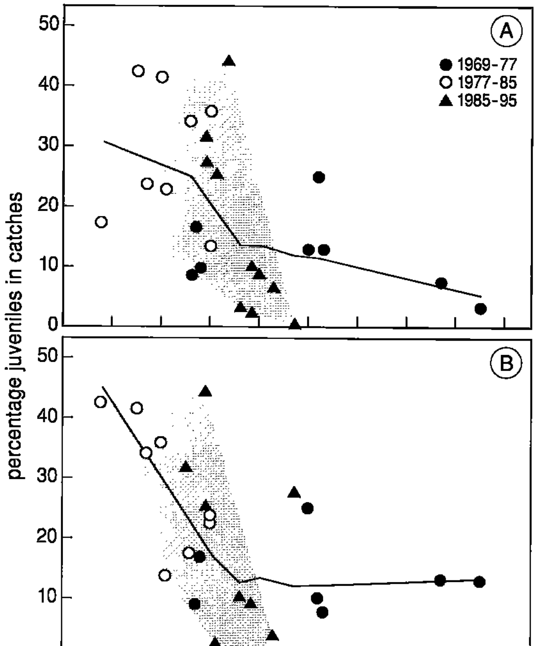

Fig. 2. The percentages juvenile Knots as a function of the UK population indices in concurrent (A) and previous (B) winters during the three different periods between 1969 and 1995. The trendline is based on the LOWESS-routine in SYSTAT (tension = 0.8). The shaded area covers the data points below the bend in the trendline to indicate the somewhat tighter fit between percentage juveniles and winter index in panel B compared to A.

Figure 2 also seems to show that the relationships between juvenile percentages and winter index numbers differ between periods. Indeed, multivariate analyses show that in addition to the significant effects of both winter index and period (the latter being a categorical variable), there were significant interactions between winter index and period in explaining the variation in arcsin-transformed juvenile percentages. Incorporating summer temperatures in the Queen Elizabeth Islands did not improve the models. The important notion here is that the negative correlations, which suggest density-dependence processes at work, are upheld. In view of the many possible caveats of these statistics (e.g. Slade 1977; Shenk *et al.* 1998; Newton 1998), we will not pursue the analyses further.

DISCUSSION

Evidence for density-dependent processes?

The two negatively correlated variables (winter index and percentage juveniles in catches) are methodologically independent. Therefore, these correlation's cannot be statistical artefacts. Nevertheless, there could be other caveats in the analysis. If catches were higher in years when there are many birds (i.e. high winter index values), the fact that juvenile percentage are smaller in large than in small catches (Table 1) could explain the negative correlation between the index of winter numbers and the percentage juveniles (Fig. 2). Although there was indeed a correlation between the average size of the cannon-net catches on the Wash (WWRG archives) and the UK winter index ($r_{26} = 0.5$, $P < 0.05$), the expected *direct* correlation between catch size and juvenile percentage was not found ($r_{26} = -0.2$, $P = 0.24$)

The negative relationship between juvenile percentages and total numbers could also reflect density-dependent variations in the winter distribution of young and adults. Given the sparsity of sustained catching efforts in areas other than the Wash, available data are unlikely to be sufficient to confirm or to completely rule out this possibility. However, the correspondence between the percentages of young recorded in catches on the Wash (WWRG archives) and elsewhere in Britain (Underhill *et al.* 1989) seems to suggest that this is an unlikely explanation.

This leaves us with the intriguing and exciting possibility that 'recruitment' of *islandica* Knots has been strongly density-dependent. That the percentage juveniles in the autumn and winter catches is negative correlated with the population size in the concurrent as well as in the previous winter, suggests that density-dependent processes may occur sometime before (1), during (2) or after (3) the breeding season. This leaves many mechanisms open, some of which will be discussed below.

(1) There may be competition for food on the wintering grounds before departure or on the staging grounds in Iceland and Norway (Davidson *et al.* 1986; Alerstam *et al.* 1992) that results in the body condition of Knots upon departure to the High Arctic being poor in years when numbers are high. Alternatively, or in addition, larger proportions of adults may decide not to make a breeding attempt at all in years of high population, perhaps not reaching the Queen Elizabeth Islands but staying behind in West-Greenland. Studies on body masses at departure (Gudmundsson *et al.* 1991) and feeding during the stopovers (Alerstam *et al.* 1992; Piersma *et al.* 1994) have been made in far too few years to enable tests of this hypothesis.

(2) Density-dependence could also operate on the breeding grounds itself, with higher numbers attempting to breed leading to reduced productivity as the best breeding sites become filled up; the extra birds being accommodated in suboptimal habitats. Although this mechanism has received empirical support to explain density-dependence in high arctic geese (e.g. Ebbinge 1989), our own experiences in the High Arctic make it difficult to believe that this could be the case. There is so much tundra habitat that, to human observers, seems to be suitable but that is not used by Knots. In principle there could be a direct influence of predators attracted to high densities of breeding Knots, thus causing a reduction in breeding success. Again, given the fact that the highest densities of Knot nests recorded so far are in the order of 2 pairs/km^2 of bare tundra (Tomkovich & Soloviev 1996; Whitfield *et al.* 1996; Tulp *et al.* 1998) and that Knot-eggs or chicks would only contribute a minute fraction of the diet of any predator, we find this an unlikely hypothesis. This is not to say that predators are unimportant: they may well importantly affect breeding success of the Taimyr breeding population (Underhill *et al.* 1989).

(3) There could be effects of total bird density during and just after southward migration affecting foraging success and rates of fattening and subsequent survival, especially in the inexperienced juveniles. This could still take place on the tundra, on the stopover sites in Iceland and Norway, and after arrival on the wintering grounds in the Wadden Sea and the British Isles. That adults routinely migrate before the juveniles and would not initially compete for food and space may argue against this idea. Indeed, the juveniles may need to join adult flocks to 'learn the ropes'.

Changing population size: survival vs. recruitment

The indices of winter numbers, and the estimates of annual adult survival and recruitment are all affected by measurement error, or the unsoundness of the underlying assumptions. Despite these uncertainties, we believe that we can conclude that changes in adult survival have had as much of an impact on population size as changes in recruitment. A direct comparison of

Table 3. Mean annual rate of change in Knot winter index compared with mean adult mortality rate (based on recoveries and controls, Haldane's method; Table 2) and mean recruitment as measured by the percentage juveniles in the catches in the three periods 1969-77, 1977-85 and 1985-95. The datum on percentages young for the winter season 1988-89 is excluded, as $n < 100$ (Appendix 1).

	1969-77	1977-85	1985-95
% change in winter index	-8.7	+4.6	+0.9
% adult mortality per annum	23.6	19.6	14.2
% young in winter catches (recruitment)	12.1	28.8	13.8
Recruitment minus mortality (% change)	-11.5	+9.2	-0.4

the estimate of mortality and recruitment in the three periods from 1969 to 1995 (Table 3) shows that in 1969-77, when the winter index was falling by 8.7% annually, mortality was high (23.6%) and recruitment low (12.1%). Both may partly be a consequence of several cold arctic summers during this interval (Boyd 1992). In 1977-85, when the winter index was rising by 4.6% a year, recruitment was very high (28.6%) and exceeded the adult losses of 19.6% per year by almost 10%. This may have come about by the initially low adult stocks allowing high recruitment in a series of normal to warm arctic summers. In 1985-95, when the winter index fluctuated about a mean of 88 without a clear time trend, mean annual recruitment (13.8%) and mortality (a minimum average of 14.2%) seemed indeed to be in balance.

That adult survival varied so much from decade to decade goes against the dictum that adult mortality rates should be the least variable demographic parameter (Charnov 1986). That not only adult survival but also recruitment of young into the wintering population seems to determine population change in Knots, flies in the face of the general conclusion of demographic modelling of long-lived species that population size would primarily be affected by variation in adult survival (Lande 1988; Hitchcock & Gratto-Trevor 1997). The latter is indeed found in studies on some of the notoriously long-lived seabirds that show strong variation in adult survival from year to year and from decade to decade (summary in Nur & Sydeman 1999). For the Knots, the factors responsible for low recruitment may also reduce adult survival in periods when infrequent but stressful conditions occur (as when the cold arctic summers struck in the period 1969-76, Boyd 1992). In other times, as in 1985-95, some constraining factor may put an upper limit to the total population by means of density-dependent processes. The factors and the processes remain to be identified.

Conservation implications and future research

One of the most important general findings emerging from long-term population studies is that it is unusual for the same balance between births and deaths to persist for many years, especially when populations are growing and when these increasing populations affect the habitats used (e.g. Cooke *et al.* 1995), or when substantial human changes to staging and wintering areas are taking place (e.g. Fox *et al.* 1998). It seems unlikely that Knots themselves can make lasting changes to their breeding, staging or wintering habitats, although they can effectively deplete their preferred food organisms temporarily (J. van Gils & T. Piersma unpubl. data). But human influences on all the major concentration areas used by *islandica* Knots have increased greatly during the last century and especially in the last thirty years (Piersma & Koolhaas 1997; Piersma & Baker 2000), so that the future well-being of these birds is largely in human hands. Sound conservation strategies need to be based on sound data, and that is where future analyses of counting and ringing data come in.

The low and falling rates of recovery of ringed

Table 4. Declining cumulative recovery rates of British-ringed *islandica* Knots in Britain, Greenland/Iceland, France or elsewhere in Europe in 1960-69, 1970-79 and 1980-89. Numbers in brackets are recoveries per 1000 birds ringed.

Decade	Number ringed	Recovered in				Total recoveries
		Britain	Greenland/Iceland	France	elsewhere	
1960-69	18 944	120 (6.3)	50 (2.6)	19 (1.0)	26 (1.4)	215 (11.3)
1970-79	36 860	194 (5.3)	92 (2.5)	61 (1.7)	36 (1.0)	383 (10.4)
1980-89	21 602	77 (3.6)	8 (0.4)	17 (0.8)	13 (0.6)	115 (5.3)
Total	77 406	399 (5.2)	150 (1.9)	97 (1.3)	75 (1.0)	713 (9.2)

Knots in Britain (Appendix 2) and elsewhere in the range (Table 4), suggest that dependence on recovery series to estimate survival will be increasingly unsatisfactory. The use of controls looks far more promising, though the handicap imposed by the practical decision of BTO and other ringing offices not to ask for and file repeats and controls by the original ringers near the original ringing site needs to be overcome. For wader marking too, it would be more productive for groups to select topics of interest to them and to plan their operations accordingly, rather than to continue catching as many waders as possible or whatever their local objectives have been. At present there is little incentive for groups to collaborate in a designed approach, because there is a shortage of people with the time and skills needed to extract the most from the results of a clearly-focused inquiry. Perhaps more could be done to encourage collaboration between volunteer ringers and professional biologists, in universities or elsewhere, though this seems unlikely to happen without encouragement and financial support from funding agencies. Finally, it is surely important that annual recruitment samples of many wader species should be compiled. Where and how they should be collected and weighted, need to be given as much attention as has been devoted to the construction of the winter index itself.

ACKNOWLEDGEMENTS

We thank all the ringers and their teams of helpers, as well as all those that counted coastal waders in winter, for the impressive foundation they have established for analyses of the kind presented here. Funding from the Netherlands Organisation for Scientific Research (NWO), through a PIONIER-grant to TP, enabled us to buy recovery and control data from the British Trust for Ornithology; we thank the BTO for permission to use those data. We are much indebted to the Wash Wader Ringing Group for providing us, without charge, with their catch data, through the agency of Phil Ireland. We thank the Wildlife Branch of the Government of the Northwest Territories for supplying unpublished data on fox-pelt exports. HB acknowledges financial assistance and other support from the Canadian Wildlife Service of Environment Canada. Thanks to Petra de Goeij for her ever supportive companionship, and to Doug Watkins, Ron Ydenberg, Joost Tinbergen, Phil Atkinson, Bart Ebbinge, Ian Newton and Les Underhill for discussion and constructive comments. This is NIOZ-publication 3333.

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SAMENVATTING

Tussen 1969 en 1995 werd de burgerlijke stand van de in Groot-Brittannië overwinterende Kanoetstrandlopers *Calidris canutus islandica* onderzocht aan de hand van gepubliceerde gegevens over aantalsveranderingen, ringgegevens en gegevens over de percentages juveniele vogels in najaars- en wintervangsten. De oudste Kanoetstrandloper in het Britse terugmeldingenbestand had een leeftijd van ten minste 25 jaar bij het terugvangen op 1 september 1992 in de Wash (een waddengebied aan de oostkust van Engeland). Aangezien uitgerekend kan worden dat de kans dat Kanoetstrandlopers tijdens de eerste winter omkomen vier keer zo groot is als de sterftekans in latere jaren, gaat het hier alleen nog over de sterftekansen van Kanoeten die ten minste één jaar oud waren toen ze werden teruggemeld. Opgesplitst voor drie perioden (van ongeveer tien jaar) waartussen de populatietrends nogal verschilden, volgt de balans van de gemiddelde sterftekans en het jongenpercentage in grote lijnen de populatieveranderingen. Voor 1969 tot 1977, toen de winterpopulatie met 8,7% per jaar afnam, wordt het gemiddelde jongenpercentage geschat op 12,1% en de gemiddelde sterftekans op

23,6% (balans –11,5%). Voor 1977-85, toen de aantallen met 5,6% per jaar toenamen, wordt het jongenpercentage geschat op 28,8% en de sterftekans op 19,6% (balans +9,2%). Voor 1985-95, toen de populatie min of meer gelijkbleef (lichte toename van 0,9% per jaar), wordt het jongenpercentage geschat op 13,8% en de sterftekans op 14,2% (balans is –0,4%). Naarmate de poolzomers kouder waren, nam het jongenpercentage af en de sterftekans toe. De kans op terugmelding nam toe tijdens en na relatief warme winters. Hoewel voor een relatief langlevende vogelsoort zoals de Kanoetstrandloper een min of meer constante sterfte verwacht kan worden (waardoor veranderingen in broedsucces het meest bepalend zijn voor de populatiegrootte), blijkt uit onze analyses dat de aantalsveranderingen van in Groot-Brittannië overwinterende Kanoetstrandlopers zowel van sterfte- als van voortplantingsfactoren afhangen. De balans tussen sterfte en aanwas laat in de loop van 35 jaar aanzienlijke variaties zien. De negatieve correlatie tussen jongenpercentages en populatiegrootte geven sterke aanwijzingen dat er dichtheidsafhankelijke processen in het spel zijn. Het zal niet eenvoudig zijn om de factoren te ontrafelen die maken dat na winters waarin Kanoetstrandlopers zeer talrijk zijn, de kans groot is dat het broedsucces laag blijft. Niettemin is begrip van dergelijke oorzakelijke relaties tussen de ecologische processen in de overwinterings- en doortrekgebieden en de demografie van Kanoetstrandlopers en andere trekvogelsoorten van fundamenteel belang voor de onderbouwing van beheer en bescherming van de schaarse gebieden waar deze trekvogels van afhankelijk zijn.

Corresponding editor: Kees (C.J.) Camphuysen
Received: 1 October 2000, Accepted 23 November 2000

Appendix 1. Numerical values of the UK winter index of Knot numbers (from Prys-Jones *et al.* 1994, with post-1991 figures from Cranswick *et al.* 1995) and the overall percentages of juveniles found in catches on the Wash in 1969-95 (WWRG pers. comm.) and elsewhere in Britain in 1971-86 (Underhill *et al.* 1989). Note that the percentage juveniles based on catch-totals (*n*) smaller than 100 (1988-89) has not been used in any calculation.

Winter season	Winter index	% juveniles in catches	*n*
1969-70	135	3.5	5065
1970-71	103	12.9	1405
1971-72	127	7.6	3715
1972-73	100	12.9	2058
1973-74	102	24.9	1522
1974-75	78	9.8	912
1975-76	77	16.5	3136
1976-77	76	8.6	692
1977-78	58	17.3	525
1978-79	65	42.5	1634
1979-80	70	41.5	1979
1980-81	80	35.8	972
1981-82	71	22.5	240
1982-83	80	13.4	866
1983-84	67	23.6	1133
1984-85	75	34.1	516
1985-86	79	31.7	1020
1986-87	81	25.4	4080
1987-88	88	2.5	651
1988-89	93	(39.8)	83
1989-90	86	3.6	1615
1990-91	88	10.2	1281
1991-92	90	9.0	928
1992-93	97	0.5	2934
1993-94	79	27.5	3347
1994-95	83	44.3	185

Appendix 2. Numbers of Red Knots ringed in Britain each calendar year, 1960-95, with numbers of British recoveries and controls. Note that boundary years are replicated at the beginning and end of each series.

Year	ringed	year of recovery											total	found later	cum. recov. (%)
1960-68				1960	1961	1962	1963	1964	1965	1966	1967	1968			
1960	568			-	2	1	2	-	-	-	-	3	8	17	2.99
1961	59				1	-	-	-	-	-	-	-	1	-	1.69
1962	254					2	1	-	-	-	-	-	3	4	2.76
1963	2599						7	11	2	1	-	20	41	40	3.12
1964	430							-	-	1	1	2	4	3	1.63
1965	764								1	-	-	8	9	25	4.45
1966	941									5	1	8	14	17	3.29
1967	799										1	2	3	22	3.13
1968	9709											43	43	196	2.46
Total	16 123			-	3	3	10	11	3	7	3	86	126	324	2.79
1968-77			1968	1969	1970	1971	1972	1973	1974	1975	1976	1977			
1968	9709		43	23	51	30	26	11	10	6	5	4	209	30	2.46
1969	2821			3	6	12	7	2	3	1	1	-	35	6	1.45
1970	7341				17	43	23	7	9	5	4	2	110	19	1.76
1971	6846					9	20	7	13	9	6	4	68	28	1.40
1972	8036						20	14	8	10	4	5	61	53	1.42
1973	1708							2	2	3	1	-	8	11	1.11
1974	1532								9	3	2	-	14	15	1.89
1975	1862									4	3	2	9	14	1.24
1976	2336										6	4	10	27	1.58
1977	1303											3	3	20	1.76
Total	43 497		43	26	74	94	96	43	54	41	32	24	527	223	1.71
1977-85				1977	1978	1979	1980	1981	1982	1983	1984	1985			
1977	1303			3	3	2	4	1	2	-	1	3	19	4	1.76
1978	3315				11	11	8	4	4	2	4	-	44	15	1.78
1979	2578					4	7	5	2	4	1	2	25	12	1.44
1980	2493						6	5	3	-	4	6	24	22	1.84
1981	1291							3	3	-	-	-	6	7	1.01
1982	1552								-	1	4	-	5	7	0.77
1983	1608									-	-	4	4	10	0.87
1984	982										2	3	5	6	1.12
1985	1935											1	1	21	1.14
Total	17 057			3	14	17	25	18	14	7	16	19	133	104	1.39
1985-95		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995			Non-cum.%
1985	1935	1	2	5	3	3	3	-	1	3	1	-	22		1.14
1986	1443		4	6	1	3	1	-	1	2	-	-	18		1.25
1987	4461			29	8	5	-	3	1	3	1	1	51		1.14
1988	2952				2	7	3	3	1	9	2	2	29		0.98
1989	2885					3	1	3	-	6	1	2	16		0.55
1990	1716						4	2	-	4	1	1	12		0.70
1991	1649							6	1	7	-	1	15		0.91
1992	594								-	2	2	1	5		0.84
1993	3544									5	6	2	13		0.37
1994	1713										1	3	4		0.23
1995	1001											1	1		0.10
Total	23 893	1	6	40	14	21	12	17	5	41	15	14	186		0.78