

# POPULATIONS, MIGRATIONS, BIOMETRICS AND MOULT OF THE TURNSTONE *Arenaria i. interpres* ON THE EAST ATLANTIC COASTLINE, WITH SPECIAL REFERENCE TO THE SIBERIAN POPULATION

R.W. SUMMERS<sup>1</sup>, L.G. UNDERHILL<sup>2</sup>, C.F. CLINNING<sup>3</sup> and M. NICOLL<sup>4</sup>

**ABSTRACT** Three populations of Turnstone were studied. Primarily a series of comparisons was made between the Canadian-Greenland population which winters mainly in western Europe and the Siberian population which winters partly in southern Africa. There was no long term change in the size of the latter population over the period 1976 to 1989. There is evidence for site fidelity to winter quarters in South Africa. Spring migration takes place through the Mediterranean and autumn migration through the Black and Caspian Seas. There are only small differences in size between the three populations of Turnstones, but marked differences occurred in patterns of change in mass. The Siberian population has no mid-winter fattening in contrast to the Canadian-Greenland population. The annual food consumption by the Siberian birds was slightly less than the Canadian-Greenland birds. The duration of primary moult of 1Y+ Siberian birds was about 45 days longer than that of Canadian-Greenland birds; it started two months later and was less synchronized. Of first-year Siberian birds 32% of the population undergo partial wing moult whereas no first-year Canadian-Greenland birds moult.

## INTRODUCTION

The Turnstone *Arenaria interpres* is a circumpolar breeding wader comprised of two subspecies, *interpres* and *morinella*, both of which have a wide latitudinal range during the non-breeding season (Cramp & Simmons 1983). The nominate subspecies, considered in this paper, breeds from Ellesmere and Axel Heiberg Islands in the Canadian Arctic (90° W), along the coasts of northern and north-east Greenland, Scandinavia and Siberia, to Alaska (135°W). The non-breeding range includes the coasts of Europe, Africa, Asia and Australasia. Given the cosmopolitan distribution, it is likely the annual cycle differs for each part of the range.

In this paper we describe the numbers and distribution of Turnstones in southern Africa and review literature to describe the other populations on the east Atlantic coastline. We also compare the biometrics, changes in mass and moult of Turnstones wintering near the southern and northern limits

(southern Africa and Scotland) of the non-breeding range. Finally, a review of ringing data and literature is used to describe the routes and timing of migration of Turnstone populations wintering along the east Atlantic coastline.

## STUDY AREA AND METHODS

Unless otherwise stated, we refer to boreal seasons. Winter surveys were used to describe the distribution and population size in southern Africa. The dates and lengths of the coastline surveyed are listed in Summers *et al.* (1987a). Most surveys were carried out between November and January, when there are no major migrations, and when Turnstone numbers are at a stable maximum (Pringle & Cooper 1975, Spearpoint *et al.* 1988). The survey methods used are described in Underhill & Whitlaw (1977) and count data have been archived in Underhill & Cooper (1984a, 1984b, 1984c). The

coastline, other than coastal wetlands and offshore islands, was split into the following habitat categories; sand, rock (includes cobbles, boulders and bedrock), mixed (either short alternating sections of sand and rock, or bedrock exposed at low tide and backed by sand) and cliff.

Winter (January or February) and summer (June or July) surveys of Langebaan Lagoon (Fig. 1), a major southern African wetland, were made between 1975 and 1988 (Underhill 1988). Counts were made at high tide when birds congregate to roost on salt marshes and sand spits. Further details of these surveys may be found in Summers (1977), Robertson (1981) and Underhill (1987a). Seasonal changes in numbers of Turnstones were described for 4.0 km of mixed shore north of Cape Recife in the eastern Cape (Fig. 1). Counts were carried out under similar weather conditions and during ebb tide near the middle of each month between July 1981 and June 1986 (Spearpoint *et al.* 1988).

The seasonal pattern of occurrence of Turnstones in the southwestern Cape was described during five years of fieldwork for the Cape Bird Club Atlas (Hockey 1983). Observers recorded the presence of species on a quarter-degree of latitude and longitude grid in each month. The percentage of field cards recording Turnstones for the 26 coastal squares between the Olifants and Bree river-mouths (Fig. 1) was calculated for each month.

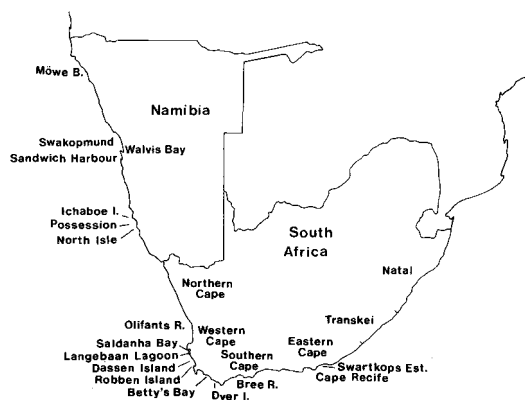


Fig. 1. Southern Africa, showing localities mentioned in the text.

Turnstones were trapped with cannon-nets, mist-nets or dazzled with torches at night. A total of 1176 were captured and ringed with South African Bird Ringing Unit (SAFRING) rings in southern Africa at Swakopmund, Olifants estuary Marcus and Vondeling Islands, Langebaan Lagoon, Betty's Bay, Botrivier Lagoon and Swartkops estuary (Fig. 1), and 1539 were captured and ringed with British Trust for Ornithology rings in eastern Scotland (Fife, Tayside and Grampian Regions). Wing length (maximum chord, Svensson 1984), measured with a stopped rule, and bill length (exposed culmen, the distance between bill tip and the junction with the feathers on the forehead) were recorded to the nearest millimetre, though latterly bill length was measured to 0.1 mm. Mass was measured to the nearest gram with a "Pesola" balance. As samples were relatively small they were weighed within a short time period. No adjustment was made to account for loss in mass between capture and weighing. Birds were aged on plumage colouration (Prater *et al.* 1977) and/or state of moult (this study). Birds in their first year of life were aged as "1Y", becoming "2Y" on 1 July when about one year old. Birds older than one year and not recognisable as 2Y were aged as "1Y+". All statistics computed for 1Y+ birds exclude birds classified as 2Y. Live birds in breeding plumage were sexed on plumage characteristics (Dementiev *et al.* 1951).

Birds were shot at Langebaan Lagoon for biometric study and body composition analyses. The following data were collected; bill length, sex (by gonad examination), fresh mass, dry mass (carcass dried to constant mass in a convection oven at 60 °C), dry fat-free mass of both pectoral muscles (pectoralis and supracoracoideus) and rest of carcass (fat removed with chloroform in a Soxhlet apparatus). By subtraction, the fat-free body mass and water mass were obtained.

Daily food consumption (*DFC*; dry mass) was estimated by Kersten & Piersma's (1987) equation

$$DFC = 4.4 + 0.09 * M + 2.1 * C - 0.27 * T$$

where the body mass *M* was interpolated for each

day from monthly or weekly average values,  $C$  was inferred from the change in daily body mass and  $T$  is average daily air temperature in °C. Average daily air temperatures were obtained for Cape Town (South Africa), Dundee (Scotland), (in the wintering areas for Siberian and Canadian-Greenland Turnstones, respectively), for the Caspian Sea and Gulf of Guinea (probable stop-over areas for Siberian Turnstones), and for the breeding areas in Siberia and Greenland.

Primary moult scores were recorded using the standard British Trust for Ornithology technique (Ginn & Melville 1983). Moult data were analysed using the assumption that rate of deposition of feather material is constant (Summers *et al.* 1983). To achieve this, the primary feathers of two Turnstones were dried for 24 hours at 100 °C, and the dry mass of each feather recorded. Results were combined to determine the mass of each primary relative to the total mass of the primaries. The statistical method used to estimate average starting and completion dates and duration of primary moult is described in Underhill (1985), Underhill & Zucchini (1988) and Underhill *et al.* (in press). In southern Africa, birds arrive, moult and then remain in the moulting area, so that the resulting data were of type 2 of Underhill & Zucchini (1988); in Scotland, two populations of Turnstones occur, one of which does not moult but occurs on passage, and would bias the samples of non-moulting birds; the resulting data were therefore taken as type 3 of Underhill & Zucchini (1988). The ten secondaries, greater coverts and five tertials were numbered from outside to inside. The 12 tail feathers were numbered in pairs from the central pair outwards. The presence or absence of actively growing body feathers, and lesser and median coverts was recorded.

An index of the amount of breeding plumage on a bird was obtained by counting the number of median coverts which were coloured chestnut-brown (breeding colours), partially coloured chestnut-brown and those which lacked chestnut-brown. The numbers of coverts in each breeding plumage class were summed for all birds within a monthly sample, and expressed as a percentage of

the total number of coverts. A similar number (c. 25) of coverts was examined on each bird.

## RESULTS

### Population size and structure

**Southern Africa** The highest densities of Turnstones occurred on the rocky shores of northern Namibia (50.3 birds per km) (Table 1). In the northern Cape densities on sandy, mixed and rocky shores were 15.8, 14.6 and 21.2 birds per km respectively. Mixed shores in the western Cape had a density of 22.2 birds per km. Densities decreased eastward along the south coast of South Africa to Natal, where the density was only 0.2 birds per km on rocky shores.

Turnstones also occurred at coastal wetlands (Tables 2 and 3). There were more than 100 Turnstones at five of 292 wetlands surveyed (87% of Turnstones at wetlands occurred at these five). Langebaan Lagoon was the most important wetland for Turnstones. Many of the offshore islands, particularly in Saldanha Bay, supported substantial populations of Turnstones (Table 4).

By combining numbers counted on the shore with numbers at coastal wetlands and on the offshore islands, we can estimate the total population for each of the regions of coastal southern Africa (Table 1). The surveys of southern Namibia, the northern Cape and Transkei were not complete. For the northern Cape and Transkei, estimates have been made by assuming that the density on the unsurveyed sections of these regions was the same as on the surveyed sections. The Turnstone population for southern Namibia has been conservatively estimated to be 5000 birds. The total winter populations for Namibia and South Africa are thus approximately 15000 and 19000 respectively.

The population in midwinter at Langebaan Lagoon fluctuated between 725 and 2766 between 1976 and 1989 (Table 3). There was no evidence for a long-term trend in midwinter population size. The summer population at Langebaan Lagoon varied between 215 and 1904 and was comprised of non-breeding first-year birds and also some presumed

**Table 1.** Lengths of coastline surveyed, Turnstone numbers and densities (numbers per km) on sections of the coast of southern Africa (Fig. 1), and numbers at coastal wetlands and offshore islands. Percentage of shoreline surveyed in each section is given in parentheses

		Sand	Mixed	Rock	Cliff	Wetlands	Offshore islands	Total counted	Total estimate	Sources
Northern Namibia (100%)	no	1184	1588	5564	-	1515	-	9851	10000	1,2,3
	density	3.2	5.2	50.3	-					
Southern Namibia (8%)	no	0	374	103	-	16	686	1179	5000	4,5,6,7
	density	0	12.0	6.9	-					
Northern Cape (40%)	no	594	1229	969	0	1	-	2793	6000	8
	density	15.8	14.6	21.2	0					
Western Cape (100%)	no	514	1642	1413	0	1710	1488	6767	7000	9,10
	density	2.1	22.2	9.5	0					
Southern Cape (88%)	no	201	560	1443	0	72	396	2672	3000	9,10,11
	density	0.8	3.4	6.4	0					
Eastern Cape (98%)	no	59	970	258	-	502	3	1792	2000	7,11
	density	0.2	7.0	5.1	-					
Transkei (50%)	no	0	94	31	0	0	-	125	250	12
	density	0	1.5	0.9	0					
Natal (99%)	no	3	87	5	-	832	-	927	1000	13
	density	0.0	0.3	0.2	-					
Total (75%)	no	2555	6554	9786	0	4648	2239	26106	34000	
	density	1.7	5.7	14.9	0.0					

Sources. 1 Underhill & Whitelaw 1977, 2 Whitelaw *et al.* 1978, 3 Ryan *et al.* 1984, 4 Cooper *et al.* 1980, 5 Hockey 1982, 6 Williams 1987, 7 WCWSG unpubl. data, 8 Ryan & Cooper 1985, 9 Summers *et al.* 1976, 10 Ryan *et al.* 1988, 11 Underhill *et al.* 1980, 12 P.A.R. Hockey unpubl. data, 13 Ryan *et al.* 1986.

second-year birds (identified on their fresh plumage compared with first-year birds). The numbers showed evidence of a three-year cycle; in 1974 (Pringle & Cooper 1975), 1977, 1980, 1983 and 1986, the summer population was more than half the population the previous winter; in 1975, 1978, 1981,

1984 and 1987, it was less than a quarter; in the remaining years, the oversummering proportion showed no pattern (Table 3). In several years the summer population approached or even exceeded the winter population. This provides further evidence in support of the suggestion by Pringle &

**Table 2.** The numbers of Turnstone counted at wetlands in southern Africa during winter (Underhill & Cooper 1984b) (Fig. 1). Only coastal wetlands supporting more than 100 Turnstones are listed. The value for Langebaan Lagoon is the median of 14 counts, whereas only a single count was carried out at the other sites

Locality	Number
Swakopmund saltworks	478
Walvis Bay Lagoon	698
Sandwich Harbour	200
Langebaan Lagoon	1926
Swartkops Estuary and associated saltworks	321

**Table 4.** The numbers of Turnstones (based on single surveys) on offshore islands in southern Africa during winter (Cooper *et al.* 1980, Ryan *et al.* 1988, LGU pers. obs) (Fig. 1) Only islands with over 75 Turnstones are listed. Malgas, Marcus, Jutten and Schaapen Islands are in Saldanha Bay

Island	Number
Ichaboe	128
North Isle	103
Possession	198
Malgas	79
Marcus	121
Jutten	83
Schaapen	235
Dassen	416
Robben	517
Dyer	396

**Table 3.** The numbers of Turnstones at Langebaan Lagoon in winter (single count in January or February each year) and summer (single count in June or July each year), and percentage of first-year birds in trapped samples in southern Africa and Scotland in winter (i.e. year 1973 refers to winter 1972-73). The summer populations at Langebaan Lagoon have been expressed as percentages of the population the previous winter

Year	Winter	Summer	Percentage oversummering	Percentage 1Y in winter ( <i>n</i> )	
				Southern Africa	Scotland
1973			54.9 *	22.2 (9)	6.0 (83)
1974			180.1 *	50.0 (4)	14.5 (338)
1975		215	11.2 **	0.0 (24)	30.2 (96)
1976	968	766	79.1	23.3 (30)	
1977	1861	1904	102.3	54.5 (433)	7.1 (140)
1978	1976	260	13.2	19.1 (58)	
1979	2075	1002	48.3	11.3 (61)	9.4 (267)
1980	2625	1365	52.0	19.8 (81)	25.0 (24)
1981	1653	215	13.0		
1982	1790	296	16.5		14.8 (81)
1983	1695	1410	83.2		17.9 (168) 17%+
1984	2536	582	22.9	28.6 (14)	22.1 (104) 18%+
1985	1990	705	35.4	24.0 (25)	19.9 (331) 26%+
1986	2766	1680	60.7		20.4 (279)
1987	725	18	2.5	0.0 (6)	16.5 (127)
1988	1876	39	2.1		
1989	2382				

\* from Pringle & Cooper (1975)

\*\* estimated as a percentage of the median winter count

+ from Whitfield (1985)

Cooper (1975, 1977) that there is an immigration of overwintering birds into the protected shores of Langebaan Lagoon, perhaps from the open shoreline and/or the islands in Saldanha Bay which are subject to frequent storms during the austral winter.

The pattern of population changes at Cape Recife was quite variable from year to year, though in three years the main influx of immigrants took place between September and November, and as late as January in one year (Fig. 2). The time of emigration was less variable: in most years it took place between March and May. The overwintering population varied between two and 80 birds. The southwestern Cape atlas data showed that from October through to March between 23% and 28% of the coastal field cards recorded Turnstones and, from May to August 10% to 12%, indicating arrival in September and departure in April (Fig. 3).

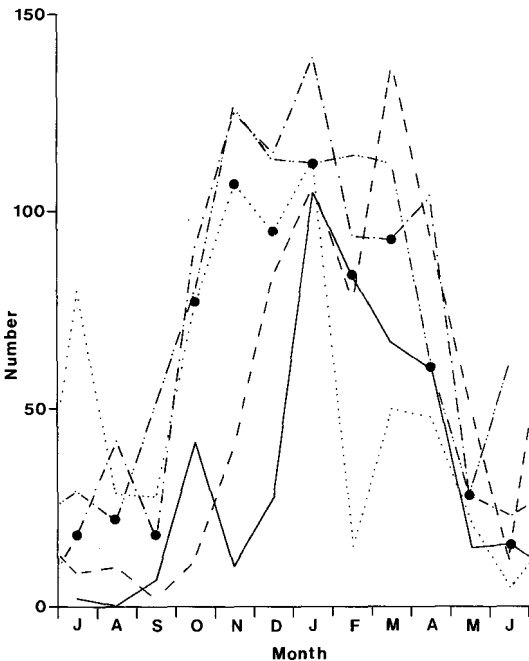


Fig. 2. Seasonal changes in the numbers of Turnstones on 4.0 km of beach between Cape Recife and Flat Rocks roadhouse (eastern Cape) for the years 1981-82 (—), 1982-83 (- - -), 1983-84 (.....), 1984-85 (-.-.-) and 1985-86 (-.-.-). Large dots show median values for each month.

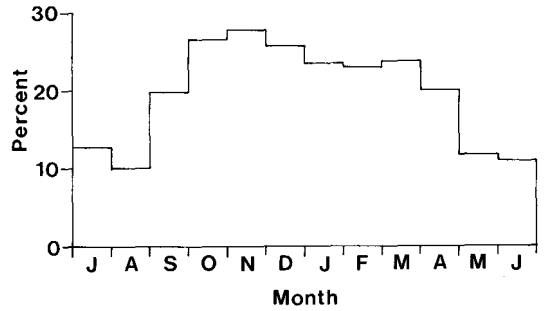


Fig. 3. Seasonal changes in the percentage of field cards recording Turnstone for the coast of the southwestern Cape.

In the southwestern Cape (primarily Langebaan Lagoon), 46 out of 89 Turnstones collected were male, and in the eastern Cape and Natal, 47 out of 89 were male. In neither sample was the sex ratio significantly different from 1:1 ( $\chi^2 = 0.1$  and 0.4 respectively,  $P > 0.05$ ). The percentage of first-year birds captured in winter in southern Africa was variable from year to year (0% - 54.5%) but small sample sizes in most years make it difficult to determine any pattern (Table 3). However, in the years 1974 and 1977, when the percentage of first-year birds in samples captured in winter exceeded 50%, the overwintering population at Langebaan Lagoon was larger than the population size the previous winter. In 1975 and 1987, when no first-year birds were trapped, low percentages of overwintering birds were recorded (Table 3).

**Scotland** The percentage of first-year Turnstones wintering in Scotland ranged from 6% to 30% between years. Large samples were obtained each year from 1982 to 1987 and there was no evidence that the variation followed a cyclic pattern (Table 3).

**Migrations and site fidelity in southern Africa**

**Site fidelity** One Turnstone was recovered nine seasons after ringing 8 km from the ringing site at Swakopmund, Namibia, and a total of 30 1Y+ Turnstones was retrapped at the site of ringing at least one month after initial capture. Nine were retrapped within the season (September-April) of rin-



**Table 6.** Bill and wing lengths (mm) of 1Y+ male and female Turnstones in southern Africa during March and April

	Male				Female			
	Mean	SD	Min-Max	<i>n</i>	Mean	SD	Min-Max	<i>n</i>
Bill length	21.6	0.8	19.5-23.2	39	22.8	0.8	21.4-24.0	19
Wing length	156.8	3.0	151-166	38	161.4	2.5	158-167	19

SD = 1.0, *n* = 132), when the feathers on the forehead are in moult (Western Cape Wader Study Group unpubl. data). However, there was no seasonal difference during winter in Scotland ( $F_{6,788} = 2.5$ ,  $P > 0.10$ ). The mean bill length of Turnstones in Scotland was significantly longer than in southern Africa; for 1Y+ birds the difference in mean bill lengths was 0.8 mm ( $t = 13.4$ ,  $P < 0.001$ ), and for first-year birds was 0.5 mm ( $t = 4.7$ ,  $P < 0.001$ ). Females had longer bills than males in southern Africa ( $t = 5.4$ ,  $P < 0.001$ ) (Table 6).

**Wing length** Measurements of new primaries of 1Y+ Turnstones in Scotland (November to January mean 158.7 mm, SD = 4.0, *n* = 215) were close to the same measurement in southern Africa (April mean 158.3 mm, SD = 3.8, *n* = 102). However, wings with worn primaries in Scotland averaged 156.2 mm (SD = 4.0, *n* = 51) (August and September), significantly longer than in southern Africa (November to January mean, 153.3, SD = 4.4, *n* = 136) ( $t = 5.3$ ,  $P < 0.001$ ). The 3 mm difference is presumably due to wear attributable to flying an extra 20000 km from and to southern Africa. A similar pattern was present in the first-year birds; southern African first-year birds had mean wing lengths (150.1, SD = 4.3, *n* = 242) 4.3 mm shorter than Scottish first-year birds (154.4, SD = 4.1, *n* = 215). Females had longer wings than males in southern Africa during spring when their primaries were new ( $t = 5.78$ ,  $P < 0.001$ ) (Table 6).

**Body mass** Turnstones displayed large seasonal variations in body mass (Table 7). In Scotland, the

mean mass of 1Y+ birds during the coldest months (December to February) was 111.3 g, whilst in southern Africa, during these hot months, the mean mass was 99.6 g, 11.7 g less. Scottish 1Y+ Turnstones increased in mass to 153.2 g in mid May, while in southern Africa the highest mean was 163.6 g. The means for May need not represent the emigration mass at departure, since birds which are still accumulating fat will reduce the means. The five heaviest masses we recorded in Scotland were 169 g, 164 g, 162 g, 160 g, and 160 g (between 5 and 17 May) and in southern Africa were 190 g, 185 g, 184 g, 182 g and 181 g (between 27 April and 13 May).

First-year birds in Scotland were about 10 g heavier during November and December than their southern African counterparts. The lowest immigration masses of first-year birds in both southern Africa and Scotland was about 84 g. Some first-year birds in Scotland underwent pre-migratory fattening (141 and 144 g on 5 May) (Table 7). Differences in mass between age classes during the period October to February were significant in Scotland ( $F_{1,811} = 16.3$ ,  $P < 0.001$ ) (1Y, 106.4 g; 1Y+, 109.9 g), but not in southern Africa ( $F_{2,513} = 1.04$ ,  $P > 0.20$ ) (1Y, 99.4 g; 2Y, 99.2 g; 1Y+, 100.3 g). An analysis of the body composition of southern African birds showed that most fluctuation in body mass was due to changes in the mass of fat (Table 8). When 1Y+ birds arrived in southern Africa in September they had moderate amounts of fat which were lost during the winter. A large amount of fat was accumulated during March and April prior to departure and the size of the pectoral muscles also increased slightly. First-



**Table 7.** Masses (g) of different age classes of Turnstones in southern Africa (SA) and Scotland (Sc)

	1Y				2Y				1Y+			
	Mean	SD	Min-Max	<i>n</i>	Mean	SD	Min-Max	<i>n</i>	Mean	SD	Min-Max	<i>n</i>
Jul	SA				100.8	6.9	87-120	60				
	Sc											
Aug	SA				100.0	-	100	1				
	Sc	112.7	13.2	96-135					113.4	10.7	96-155	91
Sep	SA				105.0	7.6	90-122	28	113.5	6.6	107-124	8
	Sc	108.7	14.8	83-147					109.7	7.9	84-135	148
Oct	SA	84.0	-	84	97.4	6.5	90-110	25	104.0	6.9	94-121	11
	Sc	104.5	8.7	81-126					109.4	8.1	89-130	264
Nov	SA	99.3	7.5	89-114	101.8	5.2	90-110	18	106.8	7.3	92-118	19
	Sc	109.1	5.1	100-118					110.6	8.0	94-132	143
Dec	SA	98.9	6.5	84-111	99.8	6.5	91-110	9	99.1	6.2	85-116	87
	Sc	109.4	12.4	84-137					113.1	9.0	95-135	119
Jan	SA	99.3	7.6	82-129	98.9	4.4	92-106	19	100.1	7.0	84-128	130
	Sc	105.7	6.1	95-115					109.4	7.3	91-125	54
Feb	SA	102.2	13.2	82-130					98.6	6.5	89-116	24
	Sc	102.6	7.3	94-118					107.1	7.3	91-125	122
Mar	SA	97.5	5.9	85-110					114.6	11.2	94-150	111
	Sc	104.3	7.2	90-115					106.8	6.1	92-123	148
Apr	SA	99.3	6.7	84-113					147.9	20.4	100-190	128
	Sc	100.8	7.4	87-108					107.8	7.0	86-123	65
May	SA	103.5	8.5	85-122					163.6	12.2	135-185	23 (1-17th)
	Sc	103.2	4.8	93-112					132.5	12.8	103-164	83 (4-6th)
	Sc	142.5	-	141-144					153.2	12.8	124-169	9 (14-17th)
Jun	SA	103.7	13.9	92-119								

year birds also increased their fat reserves in April, but only by a small amount and presumably did not migrate.

#### Annual food consumption

Food consumption was estimated for Siberian and Canadian- Greenland Turnstones from 20 July

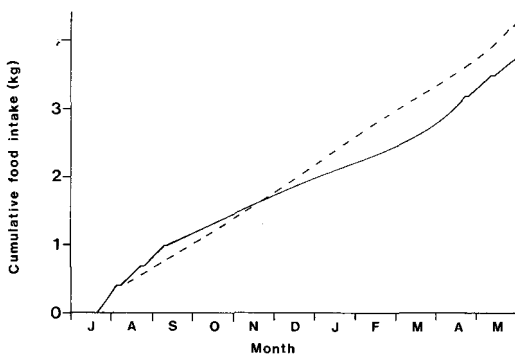
to 29 May in which the both populations undertook two periods of premigratory fattening (one for each migration) but the former undertook four additional periods of fattening during migration stop-overs (Fig. 5). Thus, food consumption on the breeding grounds after arrival and prior to premigratory fattening was not accounted for; it is probably similar

**Table 8.** The body composition of Turnstones collected at Langebaan Lagoon

		Dec- Jan	Apr	May- Aug	Sept	Oct- Nov	Dec- Jan	Mar	Apr		
Age class		1Y	1Y	1Y-2Y	1Y+	1Y+	1Y+	1Y+	1Y+		
Sample size		2	4	10	8	16	12	13	9		
Fresh body mass (g)	Mean	104.5	109.3	109.5	113.3	106.8	103.9	120.4	157.9	$F = 41.9$	$P < 0.001$
	SD	5.0	6.2	10.8	6.8	6.8	10.2	11.6	16.7		
Fat mass (g)	Mean	4.1	13.0	6.7	11.5	5.9	5.5	15.9	54.3	$F = 101.0$	$P < 0.001$
	SD	0.4	1.3	2.1	1.4	2.3	2.0	8.5	11.9		
Lean body mass (g)	Mean	100.4	96.3	102.8	101.8	100.8	98.4	104.4	103.6	$F = 1.5$	$P = 0.220$
	SD	5.4	5.4	10.1	6.1	5.8	8.9	5.9	6.7		
Dry fat free pectoral muscles (g)	Mean	5.1	5.5	5.4	5.7	5.4	5.4	5.5	6.0	$F = 2.8$	$P = 0.036$
	SD	0.8	0.7	0.5	0.5	0.4	0.5	0.5	0.4		

Note: The analyses of variance were performed on the 1Y+ birds only.

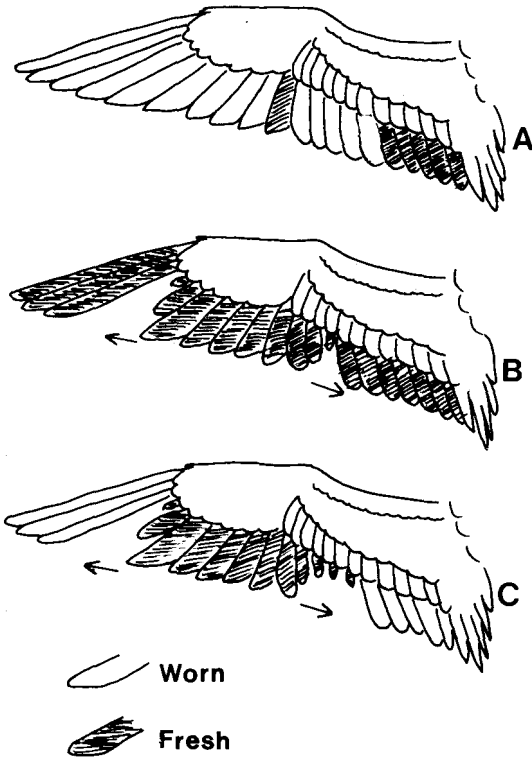
for the two populations. The total annual consumption was 3.81 kg and 4.27 kg for the Siberian and Canadian-Greenland birds respectively (Fig 5). Thus the Siberian birds eat c. 10% less though their food requirements for migration are so much greater. The benign conditions experienced in southern Africa compensate for this; daily food consumption in January is 40% less for Siberian birds than Canadian-Greenland birds.



**Fig. 5.** The estimated cumulative food consumption by Siberian (—) and Canadian-Greenland Turnstones (---) between July and May.

## Moult

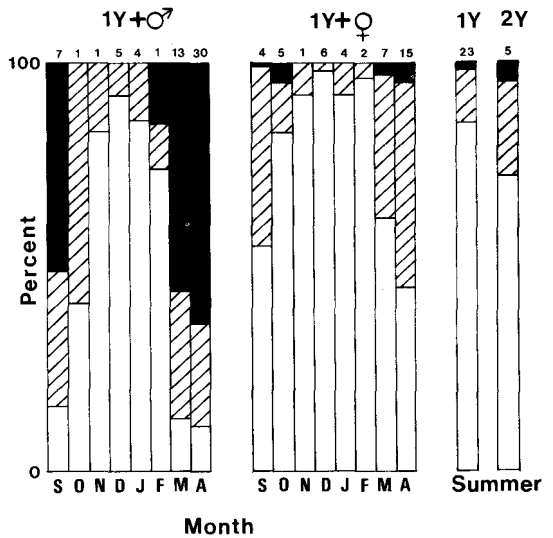
**Southern Africa** First-year birds were caught in small numbers in October and November. Their wing feathers appeared new since the feathers had been used for only one flight from the breeding grounds. No moult of primary feathers was observed until January when 2.8% of a sample of 177 were found to be in early stages of primary moult. The next samples were caught in summer when it was found that several birds had arrested moult. Usually one or two inner primaries, though as many as six, were replaced. However 17 (68%) of the first-year birds did not moult any primaries before their first summer. Moult of the secondary feathers also started in January; 2 (3.6%) birds out of 55 examined had moulted secondary 8, followed by 10. The sequence thereafter was not established but the moult of the inner secondaries was arrested. By summer, up to five secondaries were replaced (Fig. 6A). Tertiary and tail moult started in December for some birds. Moult of median wing coverts was noted in one of two birds in December, all six birds in January and was still present in four out of six birds in April, but was not recorded for three



**Fig. 6.** Patterns of moult observed in the primaries and secondaries of different age classes of Turnstones in southern Africa; A, first-year bird in arrested primary and secondary moult during its first austral winter; B, the second moult of a 2Y bird, when the outer primaries and inner secondaries, grown during the first moult, are still fresh; C, normal progression of moult in an adult bird.

birds in June. Both sexes obtained traces of breeding plumage on the median coverts by April though not as much as was observed on 1Y+ birds in April (Fig. 7). Moult of body feathers was noted from November onwards throughout the first year.

First-year birds became second-year birds on 1 July, and in about August continued their first moult of the primary feathers if they had arrested moult for summer, or started primary moult if they had summered with worn wing feathers (juvenile feathers). One second-year bird was found to have completed its first primary moult by mid-October whilst others were not yet half way through. At this



**Fig. 7.** Seasonal change in the percentage of median coverts with complete chestnut brown colouring (black), partial chestnut-brown (hatched) and no chestnut-brown (open bars), for 1Y+ males and females (sexed on dissection and on head and breast plumage in April), and for first-year and second-year birds in winter, in southern Africa. The number of birds examined is shown at the top of each bar.

time, some second-year birds embarked on their second primary moult, which proceeded in the usual way (ascendant). Normally, the first moult was completed before the second started, but one bird was observed moulting primaries for the second time before the first primary moult was completed. The second moult was often slow, with only one feather growing at a time in the latter half. Some second-year birds did not finish their second moult until late April when most 1Y+ birds were preparing for northward migration. These second-year birds could be identified by their outer primaries from their first moult, which looked fresh and showed little contrast with the inner new primaries of the current second moult (Fig. 6B). Therefore, some second-year birds were not ready to migrate at the end of their second year, and would presumably spend a second summer in the southern hemisphere before migrating north for the first time.

The breeding birds began to arrive in southern Africa during the second half of September and their plumage was worn and faded. For example, the distal halves of the chestnut median coverts were almost worn to the shafts, and their colour was much paler. There was no evidence to suggest that they had started moult of any tract during their stop-overs on southward migration. On arrival they immediately started an extensive moult of the body feathers which was followed shortly by the moult of the tertials and primaries. Primary moult took place in the normal ascendant manner (Fig. 6C). The analysis of the timing of moult initially involved transforming moult scores to percentage feather mass (Table 9). Because it was difficult to distinguish the oversummering birds from the breeding birds the analysis of moult duration was performed on all 1Y+ birds. The mean starting date for primary moult was 9 October (S.E. 5 days), the duration was 119 days (S.E. 6 days) and completion date was 5 February (S.E. 5 days) (Table 10, Fig. 10). 95% of the 1Y+ birds started moult between 8 August and 9 December.

Moult of secondaries started in November when the primary moult was half way completed and was finished by January. Tertials were found moulting in all months (except April) during the stay of the 1Y+ birds. Having moulted out the worn tertials with breeding plumage into those with non-breeding plumage, they proceeded to grow tertials with breeding plumage again. Only tertials 2 to 5 were moulted twice and the first tertial did not attain breeding plumage. Tail moult started in Octo-

**Table 9.** Masses (mg) of Turnstone primaries. Bird 1, Scotland, (Summers 1980), Bird 2, Shetland, January 1985

Primary	Bird 1		Bird 2		mean %
	Dry mass	%	Dry mass	%	
1	18	4.26	17.5	4.18	4.22
2	19	4.49	20.3	4.85	4.67
3	25	5.91	24.9	5.95	5.93
4	30	7.09	30.4	7.27	7.18
5	37	8.75	35.9	8.58	8.67
6	44	10.40	43.9	10.49	10.44
7	50	11.82	51.1	12.22	12.02
8	58	13.71	56.8	13.58	13.65
9	66	15.60	63.3	15.13	15.37
10	76	17.97	74.2	17.74	17.86

ber and was completed by February. Growth of median coverts and body feathers was recorded in all months except April. The birds moulted out of breeding plumage (last seen in December), replaced it with non-breeding plumage, and then moulted back into breeding plumage (Fig. 7).

**Scotland** The mean starting date of primary moult was 5 August (S.E. 3 days), with 95% starting between 1 July and 19 August, the duration of moult was 74 days (S.E. 4 days), and mean completion date was 19 October (S.E. 2 days) (Table 10, Fig. 10). 95% of the 1Y+ birds completed moult by 13 November. The duration of primary moult

**Table 10.** The parameters of primary moult of 1Y+ Turnstones, estimated by the method of Underhill & Zucchini (1988). Standard errors (in days) of estimates given in parentheses. *n* sample size.

site	<i>n</i>	starting date			duration	completion date	
		mean	SD (days)	95% range	mean (days)	mean	95% range
Southern Africa	577	9 Oct. (4.6)	31.5 (1.6)	8 Aug. - 9 Dec.	119.4 (5.8)	5 Febr. (5.5)	5 Dec. - 8 April
Scotland	457	5 Aug. (2.6)	12.9 (0.6)	11 July - 30 Aug.	73.8 (4.1)	19 Oct. (1.9)	24 Sept. - 13 Nov.

for Scottish birds was 46 days shorter than for southern Africa. This difference is significant (S.E. of difference = 7.1 days,  $z = 6.4$ ,  $P < 0.001$ ). The length of the 95% confidence interval of starting dates in Scotland was 51 days, compared to 123 days in southern Africa, where the spread of moult scores on any given day was much larger than in Scotland.

## DISCUSSION

### Populations and migrations

The breeding range of the *interpres* subspecies of Turnstone which uses the east Atlantic coastline can be split into three parts; the north-east Canadian (Ellesmere and Axel Heiberg Islands)-Greenland population, the Fenno Scandian-west Russian population, and the Siberian population which breeds from the Kara Sea eastward along the Siberian coast (Cramp & Simmons 1983) (Fig. 8). The region where the last population merges with those Turnstones which winter around the Indian Ocean is unknown.

**Canadian-Greenland Population** The population size and migration of the Canadian-Greenland population are better known than the other two populations. Meltofte (1985) estimated that there were a minimum of 50000 breeding individuals in Greenland and Canada, leading to a post-breeding population of 120000. This population winters mainly in northwest Europe (Branson *et al.* 1978) (Fig. 8) where c. 65000 Turnstones occur (Table 11), but also in west Africa. Because there is a difference of 55000 between the estimated post-breeding population and the wintering population, and the percentage of first-year Turnstones wintering in Britain is only about 10-20% (Table 3, Whitfield 1985), there are clearly some errors. Either the estimated size of the breeding population is too high, or the estimate of the number of young produced is too high, or there is a high juvenile mortality or the young winter elsewhere. Alternatively, as part of this population winters in west Africa (Clapham 1979, Ens *et al.* 1989) and the coastline of Norway

has yet to be surveyed for waders, the estimate of 65000 wintering birds is perhaps too low for this population. When Turnstones leave Greenland and Canada, a few adults stop-over in Iceland during late July and August, whereas first-year birds migrate through Iceland from mid August to September (Wilson 1981, Whitfield & Magnusson 1987). Arrival in Britain and on the continental coast south of southwestern Norway occurs during August (Branson *et al.* 1978, Meltofte & Rabøl 1977) (Fig. 8).

Northward migration of this population takes place in May, and the birds which have wintered in Britain leave directly from their wintering areas, rather than having incipient northward movements prior to migration (Moser & Carrier 1983, c.f. with Ferns 1981). The migrants that depart from Britain early in May have only moderate amounts of fat (mean mass of 130 g) (Branson *et al.* 1979, Table 7), sufficient for the 1500 km flight to Iceland where

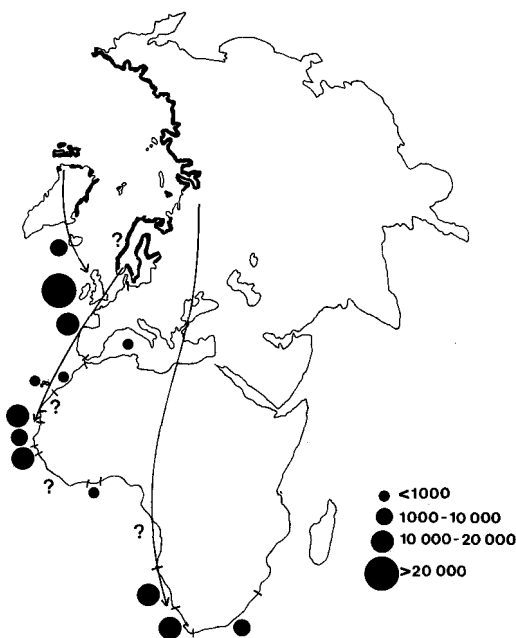


Fig. 8. The breeding range of the *interpres* subspecies of Turnstone (thick lines), and the major migration routes of the populations wintering on the east Atlantic coastline.

**Table 11.** The estimated numbers of Turnstones on the east Atlantic coastline during winter

Locality	Number	Source
Iceland	1000+	Wilson 1982
Ireland	5000+	Hutchinson 1979
Britain	44500	Moser 1987
Atlantic coasts of continental Europe (Denmark - Spain)	11000	Smit in press a
Mediterranean Basin	500	Smit in press b
Western Europe	65000	
Morocco Atlantic coast	3-400	Blondel & Blondel 1964
Morocco Atlantic coast	400	Kersten & Smit 1984
Canary Islands	780	Piersma 1986b
Banc d'Arguin, Mauritania	17000	Altenburg <i>et al.</i> 1982
Banc d'Arguin, Mauritania	6000	Trotignon <i>et al.</i> 1980
Senegal Atlantic coast	>610	De Smet & Van Gompel 1979
Senegal Saloum Delta	1-2000	Dupuy & Verschuren 1978
The Gambia	500	B. Little <i>in litt.</i>
Guinea-Bissau	15000	Zwarts 1988
Ghana	300	Ntiama-Baidu & Grieve 1987
Western Africa (max. values)	43000	
Namibia	15000	This study
South Africa	19000	This study
Southern Africa	34000	

they replenish fat reserves. Morrison (1975) recorded an average mass of 117 g on 3 May in Iceland when migrants are arriving, and 158 g on 23 May. In the last days of May, just prior to onward migration to northwest Greenland and Canada, masses of 180-190 g are common in Iceland (max. 201 g) (Wilson *in litt.*). The Turnstones which depart from Britain in mid to late May accumulate much greater fat reserves (mean masses of 150-160 g), and are thought to migrate the 2500 km to northeast Greenland in one flight, thus by-passing Iceland (Clapham 1979, Wilson 1981, Table 7). It would appear that the masses attained in Iceland exceed those attained in Britain although the distance between

Iceland and north east Greenland is only c. 1000 km (2500 km to Ellesmere Island). It is likely that high fat loads are also used as insurance against bad weather and food shortages when arriving on the breeding grounds. Morrison (1975) found that Turnstones arriving on Ellesmere Island had a mean mass of 113 g, but in years with bad weather (1966 and 1974) birds died and emaciated specimens (mean masses of 71 g and 59 g respectively) were found. Some first-year birds also accumulate fat reserves, indicating that they migrate with the adults (Table 7, Clapham 1979), but many remain in the wintering area. A few first-year birds summer and moult in Iceland (J.R. Wilson pers. comm.).

**Fenno Scandian-west Russian Population** The coastline of Norway, Sweden and Finland has a breeding population of 40000 birds (Piersma 1986a) and there will be additional birds on the Kola Peninsula. Their wintering area is mainly west Africa (Branson *et al.* 1978) (Fig. 8) where c. 43000 have been counted (Table 11). A few first-year birds from this population winter in Britain (Clapham 1979). Southward migration from the breeding areas takes place along the Baltic and Scandinavian coasts, through western Europe, including Britain, where Turnstones accumulate fat reserves (mean masses of 135 g) by early September (Branson *et al.* 1979). Such an accumulation of fat is insufficient to make a direct flight of 4000 km to west Africa so this migration is probably made in short stages (Fig. 8). Northward migration takes place along the coast of continental Europe, and a few individuals pass through Britain (Branson *et al.* 1978).

**Siberian Population** The size of the Siberian breeding population is unknown. Ringing recoveries in Asia (Fig. 4.) suggests that it is this population that winters in southern Africa (Fig. 8), where the wintering population size is estimated to be 34000 (Table 11). Little is known about Turnstone populations north of Namibia and south of Guinea-Bissau, so the region where Siberian Turnstones meet the Fenno Scandian Turnstones is unknown. Siberian Turnstones depart from the Taimyr Peninsula by late August (Dementiev *et al.* 1951) and pass through the Black and Caspian Seas in August and September (Fig. 4). They then perhaps cross the Sahara to the west coast of Africa (there are recoveries in Ghana and Gabon) and continue their migration along the east Atlantic Ocean coastline (Fig. 8). Some Turnstones also migrate through central Africa (recovery in Burundi in October). Most records in central Africa are concentrated along the Rift Valley (Dowsett 1980).

The population of Turnstones in southern Africa is concentrated along the western shores from Cape Point northward, whereas the southern and eastern Cape, Transkei and Natal have lower densities and smaller numbers (Table 1). This partly reflects the distribution of rocky coasts (Summers

*et al.* 1987b), the main habitat of Turnstones, but is probably mainly due to the richer invertebrate communities associated with the Benguela current which flows along the coast of south-western Africa. Part of the input of energy into shore communities on western coasts is through the stranding of broken kelp, *Ecklonia maxima* and *Laminaria pallida*, which can be deposited at rates of two metric tons (wet mass) per metre of shore per annum (Griffiths *et al.* 1983). The stranded weed is eaten by Talitrid amphipods and the larvae of the kelp fly *Fucellia capensis* which in turn are eaten by waders (Griffiths *et al.* 1983). Seasonal counts (Pringle & Cooper 1975, 1977, Martin & Baird 1987, Spearpoint *et al.* 1988, this paper) have shown that Turnstones are mainly present in South Africa from October to April, thus spending more time here than in any other part of their range. Retraps have shown that adults show site fidelity to their winter quarters. In this respect they are similar to the Canadian-Greenland population (Metcalf & Furness 1985). However, in parts of Namibia there are more passage migrants than winter visitors. For example, over 24 km of coast at Möwe Bay, northern Namibia (Fig. 1), peak densities of Turnstones occurred in autumn (September 8.4 birds/km and October 6.5 birds/km) and spring (April 7.0 birds/km and May 10.5 birds/km), whereas winter densities were lower (0.5 - 2.3 birds/km between November and February) (Tarr & Tarr 1987). In Gabon, Turnstones occur on passage southward (August to mid November) and northward (February to April) with very few in December and January.

Preparation for northward migration from southern Africa starts in mid-March with a slow accumulation of fat reserves, accelerating to 2.0 g/day in late April. Departure takes place mainly during late April, and the ringing recoveries in the Mediterranean suggest that this population does not follow the east Atlantic coast but crosses the Sahara and passes through central Europe. This route is also believed to be used by Curlew Sandpipers *Calidris ferruginea* (Elliott *et al.* 1976, Wilson *et al.* 1980) and Sanderlings *C. alba* (Summers *et al.* 1987b). Turnstones arrive on the Siberian breeding grounds in early June (Dementiev *et al.* 1951),

so the 13000 km migration from southern Africa is accomplished in about six weeks. Estimates of flight ranges (Summers & Waltner 1979, Castro & Myers in press) and the recorded performance of an individual (Thompson 1974) have shown that a single flight of 4000 km is a realistic estimate of a Turnstone's capabilities when departing with a mass of c. 165 g. Thus, the northward migration may be accomplished in three flights with two stopovers, perhaps in the Gulf of Guinea and the Mediterranean. Captive birds can increase in mass at a rate of 10-11 g/day, but the maximum rate in the field is c. 7 g/day (J.R. Wilson pers. comm.). Rates of 3-4 g/day are probably more usual (Morrison & Wilson 1972), so Turnstones could replenish fat reserves in about two weeks.

Our data indicate that there was no long-term change in the size of the wintering population of Turnstones at Langebaan Lagoon between 1976 and 1986 (Table 3), though there have been short-term fluctuations in the numbers of non-breeding birds (mainly first-year birds) which remain at Langebaan Lagoon during summer, with peaks indicating successful breeding in the previous summer in Siberia. These peaks in breeding success are identical in their frequency (three-year cycle) and timing to those exhibited by Knots *Calidris canutus*, Sanderlings and Curlew Sandpipers which also winter in southern Africa, and the Dark-bellied Brent Goose *Branta b. bernicla* which winter in

Europe. All four species breed in the same area of Siberia, where it is thought that their breeding success is affected by the abundance of lemmings *Dicrostonyx torquatus* and *Lemmus sibiricus* and their associated predators (Roselaar 1979, Summers 1986, Summers *et al.* 1987b, Summers & Underhill 1987, Underhill 1987b, Martin & Baird 1988, Underhill *et al.* in press). In years of lemming abundance (peaks in 1970, 1973, 1976, 1979, 1982 and 1985, Dorogov 1983), predators such as Arctic foxes *Alopex lagopus* fed largely on lemmings, but when lemmings were scarce the predators subsisted on eggs and chicks of birds, resulting in poor breeding success in the birds (P. Tomkovich, in Pienkowski 1983, P. Tomkovich pers. comm.). In contrast, the annual variation in the percentage of first-year birds in the Canadian-Greenland population followed no such cyclic pattern though they too breed in areas with lemming and fox populations. In north-east Greenland the lemming *Dicrostonyx groenlandicus* cycle is of four years (Braestrup 1941). However, as the Turnstones also breed in north and north west Greenland and the Canadian islands of Ellesmere and Axel Heiberg it is possible that the lemming cycles are out of phase, making it difficult to detect any effects that predators may be having on the population as a whole. Alternatively, annual variations in the breeding production from the Canadian-Greenland population may be unrelated to predation pressure.

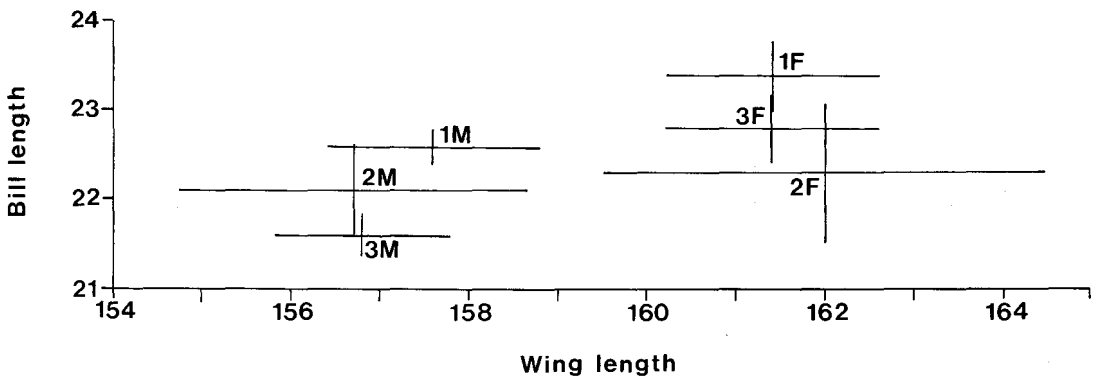
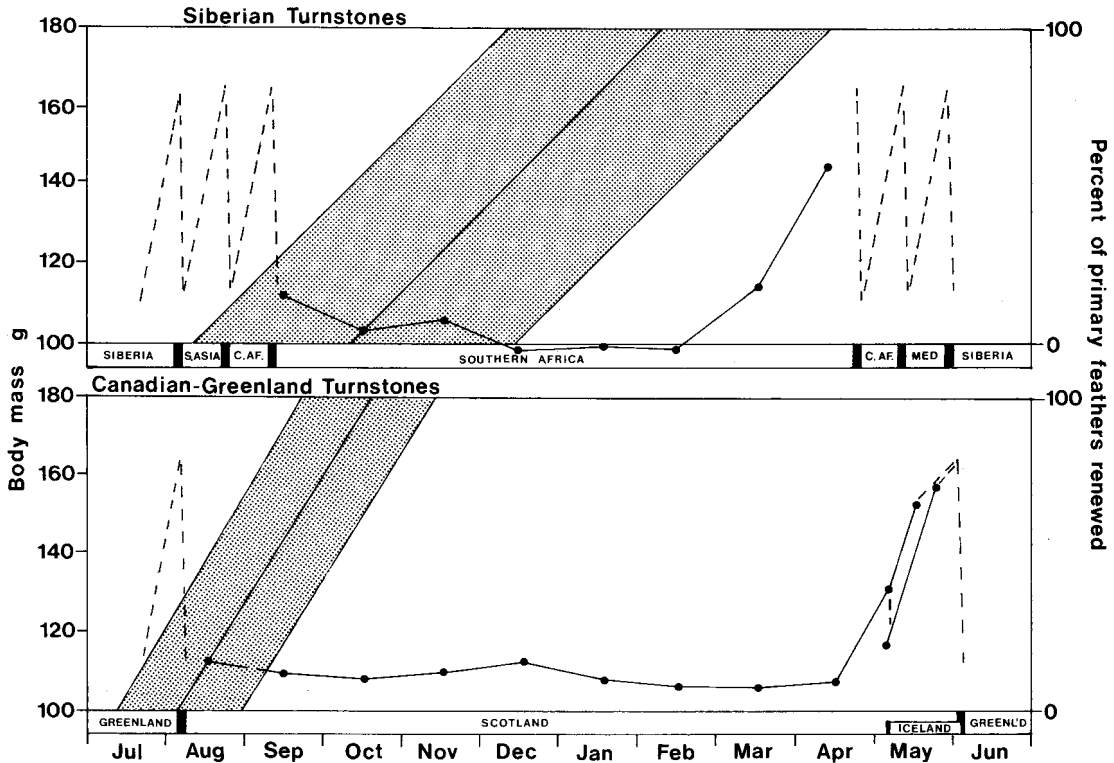


Fig. 9. Mean ( $\pm$  95% confidence limits) wing and bill lengths (mm) of 1Y+ male (M) and female (F) Turnstones from the Canadian-Greenland (1) (Whitfield 1985, fresh specimens), Fenno Scandian-west Russian (2) (Engelmoer 1984, museum specimens) and presumed Siberian (3) (Table 6, fresh specimens) populations.





**Fig.10.** Graphical model of the primary moult and mass of 1Y+ Siberian and Canadian-Greenland populations of Turnstones. The moult (from Table 10) shows the percentage of primary feather mass grown for the average bird: the parallelograms (stippled area) cover the 95% range of moult indices in the populations. The mass data (—) are from Table 7, and Wilson (*in litt.*) while migration dates are from Dementiev *et al.* (1951), Salomonsen (1950) and Morrison (1975). Hypothetical data are given in dashed lines. The apparent overlap between migration and moult is due to birds starting moult soon after they arrive and the earlier start of moult of overwintering young birds. Place names: S. Asia - southern Asia, C.Af. - central Africa, Med - Mediterranean

### Biometrics and food consumption

Comparisons of the wing and bill lengths of the three populations show that the differences in their sizes are small (Fig. 9). We found that those wintering in Scotland had slightly longer bills, but similar wing lengths to those in southern Africa (Siberian population). Thus, there has been little selective pressure on body size in the winter quarters, a factor which is believed to have led to the big differences in the sizes of individuals in the populations of Ringed Plovers *Charadrius hiaticula* wintering in Europe and Africa (Salomonsen 1955); smaller birds winter further south. Sexual differences in sizes are significant (Engelmoer 1984, Fig. 9), though Branson *et al.* (1979) concluded that dif-

ferences between sexes and ages were too small to be helpful in ageing or sexing individuals. In this study we found that bills of first-year birds in Scotland were shorter than 1Y+ birds (95% confidence interval of difference,  $0.4 \pm 0.2$  mm), but this difference was not apparent in southern Africa. The wing lengths of first-year birds were shorter than 1Y+ birds in both populations, the difference being greater in the Siberian population. Differential rates and timing of wear to the primaries make it difficult to interpret these differences.

The seasonal patterns of changes of mass varied for the different populations. The Canadian-Greenland population wintering in Europe deposit fat reserves in midwinter (fat index of about 14%)

(Branson *et al.* 1978, Johnson 1985, Whitfield 1985, Fig. 10); this strategy is thought to be a safeguard against periods of food shortage (Davidson 1981). In contrast, the Siberian population in southern Africa had low fat reserves in the warmer months (fat index of 5.3%) (mean temperature in January in Cape Town 21 °C; Table 8, Fig. 10). Fenno Scandian-west Russian Turnstones wintering in Mauritania have masses, and presumably fat loads, similar to the Siberian birds (Dick & Pienskowski 1979). First-year birds spending the austral winter in southern Africa had slightly higher fat values than 1Y+ birds in January (index of 6.1%) suggesting they respond to the cooler weather; mean July temperature in Cape Town is 12 °C. On the tropical isle of Enewetak Atoll, Marshall Islands over-summering Turnstones had a fat index of only 4.0% (Johnson & Morton 1976).

The patterns of premigratory fattening also differed between populations. For each migration, Siberian Turnstones probably go through at least three periods of fattening in about two months, and two of these periods are very short at stop-over points. In contrast, the Canadian-Greenland Turnstones fatten only once, or twice if they stopover in Iceland (Fig. 10). Therefore, the two populations have markedly different physiological cycles and energy requirements. It would seem likely that the Canadian-Greenland population may find the winter the most demanding part of the annual cycle whereas the Siberian population may find the migration periods the most demanding (Fig. 5). Our estimates of the annual food consumption indicate that the Siberian Turnstones have slightly lower annual food requirements, showing the benefit of migrating further to a benign wintering area. The estimates of food consumption are crude, being based solely on air temperatures and fat accumulation prior to migration. They take no account of the birds' behavioural responses when faced with adverse conditions. However, they do provide a first estimate of food requirements of populations with differing wintering/migration strategies.

## Moult

The moult of the first-year Siberian Turnstones

in southern Africa is peculiar in that inner primaries and secondaries may be moulted within the first year. In other wader species, first-year birds tend to moult outer primaries with inner secondaries (Elliott *et al.* 1976, Waltner 1976). The strong sunlight fades and helps to increase the wear of feathers so that there are clear advantages in maintaining flight efficiency by moulting those feathers that are most affected - the outer primaries. Therefore, it is not clear why first-year Turnstones in southern Africa have this unusual moult pattern. The first full moult is started when they are about one year old, just prior to the arrival of the 1Y+ birds. The first-year Turnstones in the Canadian-Greenland population do not moult within their first year and start their first primary moult in late summer about six weeks before the 1Y+ birds (Branson *et al.* 1979).

There have been various estimates for the duration of primary moult for the Canadian-Greenland population of Turnstones; c. 70 days in Iceland (Morrison 1976), c. 70-75 days on the Waddenzee, The Netherlands (Boere 1976), 80 days in England (Branson *et al.* 1979) and 74 days in Scotland (this study). There is one estimate for Turnstones moulting in Morocco; possibly c. 60 days (Pienkowski *et al.* 1976). Summers *et al.* (1983) have shown that widely different estimates for the duration of primary moult are obtained if different methods are used. Therefore, it is difficult to discuss the differences between the above estimates of primary moult duration in relation to different moulting areas and latitudes (Prater 1981). In this study, we used the same method to estimate primary moult parameters and found that the moult period was significantly longer and less synchronised in southern Africa (the central Siberian population) compared with Scotland (the Canadian-Greenland population) (Fig. 10). Also, primary moult in southern Africa takes place nine weeks later, a time difference that is probably related to the differences in arrival times on their wintering areas. The faster moult of the Scottish birds probably reflects the need to complete moult before the onset of cold weather in winter, when food may be less available and a full set of feathers is required for insulation.

In contrast, during the warm austral summer in southern Africa, there is less need to complete moult quickly. It spans virtually the entire winter period and is only completed just before pre-migratory fattening (average values, Fig. 10).

### Why do Siberian Turnstones migrate so far?

Gauthreaux (1982) has argued that the distribution of wintering areas for birds can be explained by dominance. Generally males dominate females, and old birds dominate young birds so that adult males attain the best wintering areas (usually further north for those birds that breed in the temperate and arctic regions of the northern hemisphere). Young females are forced to winter in poor areas further south. Pienkowski & Evans (1985) have developed this hypothesis for waders, arguing that there is intraspecific competition for wintering areas near to the breeding grounds resulting in juveniles being forced to winter further south where survival rate is perhaps lower.

The three populations of Turnstones dealt with in this paper have different but overlapping winter ranges along the east Atlantic coastline, and there are consequent differences in their annual cycles. This suggests that the migration patterns are fixed for each population. There is now evidence from ringing retraps (Elliott *et al.* 1976, Summers *et al.* 1987b, this study) and the stability in population size between years to show that localities in southern Africa represent the winter homes of many species of waders and are not overflow areas for sites further north from which they receive large numbers only in years of good breeding (Underhill 1987a). Therefore, it would be difficult to interpret the current distribution of the three populations of Turnstones in terms of competition, unless of course these patterns are a result of competition in the past.

The value of wintering close to the breeding grounds has also been put forward by Myers (1981) to explain the different wintering areas of the sexes of some waders. Sexual selection would favour those males which arrive earliest on the breeding grounds and this could be achieved by wintering further north (Myers 1981). Male Turnstones do

arrive before the females on the breeding grounds (D.P. Whitfield pers. comm.) but there has been no indication that this had led to males wintering further north; in both the Canadian-Greenland and the Siberian populations the sex ratio is one to one in their wintering areas (Whitfield 1985, this study). Thus, wintering locations need not be a constraint on the phenology of migration.

Myers *et al.* (1984) have listed the possible benefits that waders may accrue by wintering further south of conspecifics; benign wintering conditions, more predictable or abundant food supplies, less competition or less predation. For several of these features there is no comparative information. However, densities of Turnstones can be as high in South Africa as in Britain (Summers *et al.* 1975) and the numbers of other wader species higher (Summers *et al.* 1987a) so that competition could potentially be as great in southern Africa as in Europe. There is no doubt that wintering conditions in southern Africa are benign compared to northern Europe where food requirements are higher and severe weather can cause large scale mortality in waders (Davidson 1981). However, average survival rates appear to be fairly similar for at least two of Turnstone populations; 85% for the Canadian-Greenland birds (Metcalf & Furness 1985) and 78% for the Fenno-Scandian-west Russian population (Bergman 1946). There are no estimates for survival in the Siberian population as yet. The migration season may be when greatest mortality occurs in the Siberian population because many of the waders which winter in southern Africa delay the time of their first northward migration. All Curlew Sandpipers (Elliott *et al.* 1976), most Sanderlings (Summers *et al.* 1987b) and many first-year and some second-year Turnstones remain in the south during their first summer. In contrast, practically all Dunlins *Calidris alpina* (Swann 1988), all Purple Sandpipers *C. maritima* (Atkinson *et al.* 1981), and some Turnstones which winter in Europe, go north to the breeding grounds in their first summer and may breed for the first time as one year old birds (Soikkeli 1967, RWS pers. obs).

In conclusion, it is difficult from a comparison of the annual cycles to explain why the Siberian

Turnstones migrate so far. There are obvious advantages and disadvantages in this migration strategy, but we cannot say that the southern wintering birds are adopting a strategy that is inferior to that adopted by the northern wintering birds.

### ACKNOWLEDGEMENTS

We thank fellow members of the Western Cape Wader Study Group and the Tay Ringing Group who helped in trapping and counting waders: D. Abernethy, N.K. Atkinson, K. Brockie, E. Cameron, M. Chesney, J. Clark, M.A. Connor, J. Cooper, C.C.H. Elliott, J.M. Harwood, P.A.R. Hockey, P. Kemp, F. Kiddie, S. Laing, B. Lynch, M. Martin, P.M. Morant, D.W. Oliver, H.P. Pfister, J.S. Pringle, H. Robb, H.G. Robertson, P.G. Ryan, G.D. Underhill, B. Vanderwalt, M. Waltner, D.A. Whitelaw and G.H. Wilson. Additional ringing data were made available by A.P. Martin. A large number of individuals participated in surveys and we thank them all for their contributions. In particular, we thank B. Every, P.A.R. Hockey, J.A. Spearpoint and A.J. Williams for making available unpublished data. Fat analyses were carried out in Botswana by J.S.S. Beesley at the Centre for Overseas Pest Research of the United Kingdom. SAFRING provided ringing recovery data. H.L. Holgate and D.A. Priilaid prepared data for the computer. The Cape Bird Club Atlas Committee made available unpublished data from the southwestern Cape atlas.

J. Cooper, P.A.R. Hockey, A.P. Martin, N. Metcalfe, M.E. Moser, T. Piersma, P.G. Ryan, M. Waltner, D.P. Whitfield, A.J. Williams and J.R. Wilson commented on earlier drafts.

RWS acknowledges funding from 1974 to 1977 from the then South African Department of Planning and the Environment while employed by the Percy FitzPatrick Institute of African Ornithology, University of Cape Town. LGU acknowledges support from the University of Cape Town and the Foundation for Research Development of the Council for Scientific and Industrial Research especially while on study leave at Rothamsted Experimental Station, Harpenden, England.

This paper is a contribution of the Western Cape Wader Study Group and the Tay Ringing Group.

### REFERENCES

- Altenburg, W., M. Engelmoer, R. Mes & T. Piersma 1982. Wintering waders on the Banc d'Arguin, Mauritania. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.
- Atkinson, N.K., R.W. Summers, M. Nicoll & J.J.D. Greenwood 1981. Population, movements and biometrics of the Purple Sandpiper *Calidris maritima* in eastern Scotland. *Ornis Scand.* 12:18-27.
- Bergman, G. 1946. Der Steinwalzer, *Arenaria i. interpres* (L.) in seiner Beziehung zur Umwelt. *Acta Zool. Fenn.* 47:1-144.
- Blondel, J. & C. Blondel 1964. Remarques sur l'hivernage des limicoles et autres oiseaux aquatiques au Maroc. *Alauda* 32:250-279.
- Boere, G.C. 1976. The significance of the Dutch Waddenzee in the annual life cycle of arctic, subarctic and boreal waders. Part I. The function as a moulting area. *Ardea* 64:210-291.
- Braestrup, F.W. 1941. A study on the Arctic Fox in Greenland. Immigrations, fluctuations in numbers based mainly on trading statistics. *Medd. om Grøn.* 131(4):1-101.
- Branson, N.J.B.A., E.D. Ponting & C.D.T. Minton 1978. Turnstone migrations in Britain and Europe. *Bird Study* 25:181-187.
- Branson, N.J.B.A., E.D. Ponting & C.D.T. Minton 1979. Turnstone populations on the Wash. *Bird Study* 26:47-54.
- Castro, G. & J.P. Myers. in press. Flight range estimates for shorebirds. *Auk*.
- Clapham, C. 1979. The Turnstone populations of Morecambe Bay. *Ring. & Migr.* 2:144-150.
- Cooper, J., H.G. Robertson & P.D. Shaughnessy 1980. Waders (Charadrii) and other coastal birds of the Diamond Coast and the islands off South West Africa. *Madoqua* 12:51-57.
- Cramp, S. & K.E.L. Simmons (Eds) 1983. The birds of the western Palearctic. Vol. 3. Oxford University Press, Oxford.
- Davidson, N.C. 1981. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. In: N.V. Jones & W.J. Wolff (Eds.). Feeding and survival strategies of estuarine organisms. Pp. 231-249. Plenum Press, New York.
- Dementiev, G.P., N.A. Gladkov & E.P. Spangenberg 1951. Birds of the Soviet Union, Vol. 3. Israel Program for Scientific Translation, Jerusalem.
- De Smet, K. & J. Van Gompel 1979. Wader counts at the Senegalese coast in winter 1978-1979. *Wader Study Group Bull.* 27:30.
- Dick, W.J.A. & M.W. Pienkowski 1979. Autumn and early winter weights of waders in north-west Africa. *Ornis Scand.* 10:117-123.

- Dorogov, V.F. 1983. Nesting of the Rough-legged Buz-zard on Taimyr. In: Ecology and Rational Use of Land Vertebrates of North Central Siberia. Pp. 118-126, Novosibirsk.
- Dowsett, R.J. 1980. The migration of coastal waders from the Palaearctic across Africa. *Gerfaut* 70:3-35.
- Dupuy, A. & J. Verschuren 1978. Note sur les oiseaux, principalement aquatiques de la région du Parc National de Delta du Saloum (Sénégal). *Gerfaut* 68: 321-345.
- Elliott, C.C.H., M. Waltner, L.G. Underhill, J.S. Pringle & W.J.A. Dick 1976. The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. *Ostrich* 47:191-213.
- Engelmoer, M. 1984. Analyses van biometrische gegevens van 12 soorten Holarctische steltlopers. Staatsbosbeheer, Inspectie Natuurbehoud.
- Ens, B.J., T. Piersma, W.J. Wolff & L. Zwarts (Eds) 1989. Report of Dutch Mauritanian Project Banc d'Arguin 1985-1986. WIWO report 25/RIN-rapport 89/6, Texel.
- Ferns, P.N. 1981. The spring migration of Turnstones through Britain in 1979. *Wader Study Group Bull.* 31:36-40.
- Gauthreaux, S.A. 1982. The ecology and evolution of avian migration systems. In: D.S. Farner, J.R. King & K.C. Parkes (Eds.). *Avian biology*, Vol IV. Pp 93-168. Academic Press, New York.
- Ginn, H.B. & D.S. Melville 1983. Moults in Birds. BTO Guide 19. British Trust for Ornithology, Tring.
- Griffiths, C.L., J.M.E. Stenton-Dozey & K. Koop 1983. Kelp wrack and the flow of energy through a sandy beach ecosystem. In: A. McLachlan & T. Erasmus (Eds.). *Sandy beaches as ecosystems*. Pp 547-556, Dr. W. Junk, The Hague.
- Hockey, P.A.R. 1982. Waders (Charadrii) and other coastal birds in the Lüderitz region of South West Africa. *Madoqua* 13:27-33.
- Hockey, P.A.R. 1983. Atlas of the birds of the S.W. Cape - the first 15 months. *Bokmakierie* 35:80-83.
- Hutchinson, C.D. 1979. Ireland's wetlands and their birds. Dublin.
- Johnson, C. 1985. Patterns of seasonal weight variation in waders on the Wash. *Ring. & Migr.* 6:19-32.
- Johnson, O.W. & M.L. Morton 1976. Fat content and flight range in shorebirds summering on Enewetak Atoll. *Condor* 78:144-145.
- Kersten, M. & T. Piersma 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* 75: 175-187.
- Kersten, M. & C.J. Smit 1984. The Atlantic coast of Morocco. In: P.R. Evans, J.D. Goss-Custard & W.G. Hale (Eds.). *Coastal waders and wildfowl in winter*. Pp 276-292. Cambridge University Press, Cambridge.
- Martin, A.P. & D. Baird 1987. Seasonal abundance and distribution of birds on the Swartkops Estuary, Port Elizabeth. *Ostrich* 58:122-134.
- Martin, A.P. & D. Baird 1988. Lemming cycles - which Palearctic migrants are affected? *Bird Study* 35: 143-145.
- Meltofte, H. 1985. Populations and breeding schedules of waders, Charadrii, in high arctic Greenland. *Medd. om Grøn, Bioscience* 16:1-43.
- Meltofte, H. & J. Rabøl 1977. Vejnets ind flydelse på efterårstrækket af vadevugle ved Blåvandshuk, med et forsøg på en analyse af trækkets geografiske oprindelse. *Dansk Orn. Foren. Tidsskr.* 71:43-63.
- Metcalf, N.B. & R.W. Furness 1985. Survival, winter population stability and site fidelity in the Turnstone *Arenaria interpres*. *Bird Study* 32:207-214.
- Morrison, R.I.G. 1975. Migration and morphometrics of European Knot and Turnstone on Ellesmere Island, Canada. *Bird-Banding* 46:290-301.
- Morrison, R.I.G. & J.R. Wilson 1972. Cambridge Iceland Expedition 1971. Cambridge.
- Morrison, R.I.G. 1976. Moults of the Purple Sandpiper *Calidris maritima* in Iceland. *Ibis* 118:237-246.
- Moser, M.E. 1987. A revision of population estimates for waders (Charadrii) wintering on the coastline of Britain. *Biol. Conserv.* 39:153-164.
- Moser, M.E. & M. Carrier 1983. Patterns of population turnover in Ringed Plovers and Turnstones during their spring passage through the Solway Firth in 1983. *Wader Study Group Bull.* 39:37-41.
- Myers, J.P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59:1527-1534.
- Myers, J.P., J.L. Maron & M. Sallaberry 1984. Going to extremes: why do Sanderlings migrate to the Neotropics? *Ornithol. Monogr.* 36: 520-535.
- Ntiamao-Baidu, Y. & A. Grieve 1987. Palearctic waders in coastal Ghana in 1985/86. *Wader Study Group Bull.* 49, Suppl./IWRB Special Publication 7: 76-78.
- Pienkowski, M.W. 1983. A poor breeding season in 1983 for some waders on the Taimyr Peninsula. *Wader Study Group Bull.* 39:34.
- Pienkowski, M.W. & P.R. Evans 1985. The role of migration in the population dynamics of birds. In: R.M. Sibly & R.H. Smith (Eds.). *Behavioural ecology*. Pp 331-352. Blackwell, Oxford.
- Pienkowski, M.W., P.J. Knight, D.J. Stanyard & F.B. Argyle 1976. The primary moult of waders on the Atlantic coast of Morocco. *Ibis* 118:347-365.
- Piersma, T. 1986a. Breeding waders in Europe. *Wader Study Group Bull.* 48, Suppl. 1-116.
- Piersma, T. 1986b. Coastal waders on three Canary islands in March-April 1986. *Wader Study Group Bull.* 48:19-20.

- Prater, A.J. 1981. A review of the patterns of primary moult in Palaearctic Waders (Charadrii). In: J. Cooper (Ed.) Proceedings of the Symposium on Birds of the Sea and Shore. Pp 393-409. African Seabird Group, Cape Town.
- Prater, A.J., J.H. Marchant & J. Vuorinen 1977. Guide to the identification and ageing of Holarctic waders. BTO Guide 17. British Trust for Ornithology, Tring.
- Pringle, J.S. & J. Cooper 1975. The Palaearctic wader population of Langebaan Lagoon. Ostrich 46: 213-218.
- Pringle, J.S. & J. Cooper 1977. Wader populations (Charadrii) of the marine littoral of the Cape Peninsula, South Africa. Ostrich 48:98-105.
- Robertson, H.G. 1981. Annual summer and winter fluctuations of Palaearctic and resident waders (Charadrii) at Langebaan Lagoon, South Africa, 1975-1979. In: J. Cooper (Ed.) Proceedings of the Symposium on Birds of the Sea and Shore. Pp 335-345. African Seabird Group, Cape Town.
- Roselaar, C.S. 1979. Fluctuations in aantallen Krombekstrandlopers *Calidris ferruginea*. Watervogels 4: 202-210.
- Ryan, P.G. & J. Cooper 1985. Waders (Charadrii) and other coastal birds of the northwestern Cape Province, South Africa. Bontebok 4:1-8.
- Ryan, P.G., J. Cooper, P.A.R. Hockey & A. Berruti 1986. Waders (Charadrii) and other water birds on the coast and adjacent wetlands of Natal, 1980-81. Lammergeyer 36:1-33.
- Ryan, P.G., J. Cooper & C.J. Stutterheim 1984. Waders (Charadrii) and other coastal birds of the Skeleton Coast, South West Africa. Madoqua 14:71-78.
- Ryan, P.G., L.G. Underhill, J. Cooper & M. Waltner 1988. Waders (Charadrii) and other water birds on the coast, adjacent wetlands and offshore islands of the southwestern Cape Province, South Africa, summer 1980/81. Bontebok 6:1-19.
- Salomonsen, F. 1950. The birds of Greenland. Munksgaard, Copenhagen.
- Salomonsen, F. 1955. The evolutionary significance of bird-migration. Dan. Biol. Medd. 11(6):1-62.
- Smit, C.J. in press a. The importance of Iberian wetlands for waders. In: J. Castroviejo, (Ed.). Proceedings IWRB Conference, St. Maria de la Roldia, Spain, 1983.
- Smit, C.J. in press b. Waders along the Mediterranean. A summary of present knowledge. In: A. Farina (Ed.). Proceedings of 1st Conference on Birds Wintering in the Mediterranean Region, Aulla, Italy, 1984.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4:158-198.
- Spearpoint, J.A., B. Every & L.G. Underhill 1988. Waders (Charadrii) and other shorebirds at Cape Recife, Algoa Bay, South Africa: seasonality, trends, conservation and reliability of surveys. Ostrich 59:166-177.
- Summers, R.W. 1977. Distribution, abundance and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. Trans. Roy. Soc. S. Afr. 42: 483-495.
- Summers, R.W. 1980. On the rate of change of moult scores in waders. Wader Study Group Bull. 28:24.
- Summers, R.W. 1986. Breeding production of Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to lemming cycles. Bird Study 33:105-108.
- Summers, R.W., N.K. Atkinson & M. Nicoll 1975. Wintering wader populations on the rocky shores of eastern Scotland. Scott. Birds 8:299-308.
- Summers, R.W., J.S. Pringle & J. Cooper 1976. The status of coastal waders in the south-western Cape, South Africa, summer 1975-76. Western Cape Wader Study Group, Cape Town.
- Summers, R.W., R.L. Swann & M. Nicoll 1983. The effects of methods on estimates of primary moult duration in the Redshank *Tringa totanus*. Bird Study 30:149-156.
- Summers, R.W. & L.G. Underhill 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Study 34:161-171.
- Summers, R.W., L.G. Underhill, D.J. Pearson & D.A. Scott 1987a. Wader migration systems in southern and eastern Africa and western Asia. Wader Study Group Bull. 49, Suppl./IWRB Spec. Publ. 7:15-34.
- Summers, R.W., L.G. Underhill, M. Waltner, & D.A. Whitelaw 1987b. Population, biometrics and movements of the Sanderling *Calidris alba* in southern Africa. Ostrich 58:24-39.
- Summers, R.W. & M. Waltner 1979. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. Ostrich 50:21-37.
- Svensson, L. 1984. Identification guide to European passerines. Third edition. Lars Svensson, Stockholm.
- Swann, R.L. 1988. Summering shorebirds in the Moray Basin. Scott. Bird News 11:10.
- Tarr, J.G. & P.W. Tarr 1987. Seasonal abundance and the distribution of coastal birds on the northern Skeleton Coast, South West Africa/Namibia. Madoqua 15:63-72.
- Thompson, M.C. 1974. Migratory patterns of Ruddy Turnstones in the Central Pacific region. Living Bird 12:5-23.
- Trotignon, E., J. Trotignon, M. Baillou, J.-F. Dejonghe, L. Duhautois & M. Lecomte 1980. Recensement hivernal des limicoles et autres oiseaux aquatiques sur le Banc d'Arguin (Mauritanie) (Hiver 1978/79). L'Oiseau 50:323-343.

- Underhill, L.G. 1985. Estimating the parameters for primary moult - a new statistical model. Wader Study Group Bull. 44:27-29.
- Underhill, L.G. 1987a. Waders (Charadrii) and other waterbirds at Langebaan Lagoon, South Africa, 1975-1986. Ostrich 58:145-155.
- Underhill, L.G. 1987b. Changes in the age structure of Curlew Sandpiper populations at Langebaan Lagoon, South Africa, in relation to lemming cycles in Siberia. Trans. Roy. Soc. S. Afr. 46:209-214.
- Underhill, L.G. 1988. Counts of waterbirds at Langebaan Lagoon, 1975-1988. Report of Western Cape Wader Study Group, Cape Town.
- Underhill, L.G. & J. Cooper 1984a. Counts of waterbirds on the shoreline of southern Africa, 1976 to 1984. Report of the Western Cape Wader Study Group and the Percy FitzPatrick Institute of African Ornithology, University of Cape Town.
- Underhill, L.G. & J. Cooper 1984b. Counts of waterbirds at coastal wetlands in southern Africa, 1976 to 1984. Report of the Western Cape Wader Study Group and the Percy FitzPatrick Institute of African Ornithology, University of Cape Town.
- Underhill, L.G. & J. Cooper 1984c. Counts of waterbirds at the offshore islands of southern Africa, 1976 to 1984. Report of the Western Cape Wader Study Group and the Percy FitzPatrick Institute of African Ornithology, University of Cape Town.
- Underhill, L.G., J. Cooper & M. Waltner 1980. The status of waders (Charadrii) and other birds in the coastal region of the southern and eastern Cape, summer 1978/79. Cape Town: Western Cape Wader Study Group.
- Underhill, L.G., M. Waltner & R.W. Summers. in press. Three-year cycles in breeding productivity of Knots *Calidris canutus* wintering in southern Africa suggest Taimyr Peninsula provenance. Bird Study.
- Underhill, L.G. & D.A. Whitelaw 1977. An ornithological expedition to the Namib Coast, summer 1976/77. Western Cape Wader Study Group, Cape Town.
- Underhill, L.G. & W. Zucchini 1988. A model for avian primary moult. Ibis 130:358-372.
- Underhill, L.G., W. Zucchini & R.W. Summers. in press. A model for avian primary moult - data types based on migration strategies and an example using the Redshank *Tringa totanus*. Ibis.
- Waltner, M. 1976. Moulting in Palaearctic waders. Safring News 6:14-17.
- Whitelaw, D.A., L.G. Underhill, J. Cooper & C.F. Clinning 1978. Waders (Charadrii) and other birds on the Namib Coast: counts and conservation priorities. Madoqua 11:137-150.
- Whitfield, D.P. 1985. Social organisation and feeding behaviour of wintering Turnstone (*Arenaria interpres*). Ph.D. Thesis, Univ. of Edinburgh.
- Whitfield, D.P. & J. Magnusson 1987. The migration of waders through north-east Iceland. Wader Study Group Bull. 49, Supp./IWRB Spec. Publ. 7:85-89.
- Williams, A.J. 1987. Coastal bird counts along the Namib coast, Cape Cross to Lüderitz, November and December 1985. *Lanioturdus* 23:3-8.
- Wilson, J.R. 1981. The migration of High Arctic shorebirds through Iceland. Bird Study 28:21-32.
- Wilson, J.R. 1982. The wintering of shorebirds in Iceland. Wader Study Group Bull. 36:16-19.
- Wilson, J.R., M.A. Czajkowski & M.W. Pienkowski 1980. The migration through Europe and wintering in West Africa of Curlew Sandpipers. Wildfowl 31:107-122.
- Zwarts, L. 1988. Numbers and distribution of coastal waders in Guinea-Bissau. Ardea 76: 42-55.

## SAMENVATTING

Aan Oost-Atlantische kusten overwinteren drie Steenloper-populaties. In dit artikel worden in eerste instantie twee van deze drie populaties met elkaar vergeleken: de Canadees-Groenlandse populatie die vooral in West-Europa overwintert en de Siberische populatie die gedeeltelijk in Zuid-Afrika overwintert. Deze laatste populatie wordt in Namibië en Zuid-Afrika geschat op respectievelijk 15.000 en 19.000 exx. Tussen 1976 tot 1989 werden geen lange termijn veranderingen in aantalsverloop waargenomen. De sexe verhouding was 1:1. Ze arriveerden in september en oktober en vertrokken in april en begin mei. Een klein gedeelte van de eerstejaars en enkele tweedejaars vogels overzomerden. Het verloop van deze zomerpopulatie vertoonde een driejarige cyclus. De hoogste aantallen kwamen voor na lemming-jaren in Siberië. Het broedsucces wordt vermoedelijk beïnvloed door veranderingen in de prooikeuze van de Poolvossen. Verschillende Steenlopers werden voor een tweede maal in Zuid-Afrika gevangen in opeenvolgende jaren. Dit wijst op plaatstrouw aan de overwinteringsplaats. Uit ringvondsten bleek dat de voorjaarstrek plaatsvindt door het Middellandse Zee gebied en de herfsttrek door het gebied van Zwarte Zee en Kaspische Zee.

Er zijn maar kleine verschillen in de afmetingen van vleugel- en snavelengte van de onderzochte

steenloperpopulaties. Het gewichtsverloop verschilt echter opvallend: de Siberische vogels leggen in het midden van de winter geen vetvoorraad aan in tegenstelling tot de Canadees-Groenlandse populatie. De Siberische populatie legt daarentegen in drie periodes gedurende de trektijd vetvoorraden aan. De Canadees-Groenlandse populatie doet dit maar één of twee keer, omdat zij veel dichtter bij het broedgebied overwintert. Toch is de voedselconsumptie op jaarbasis van de Siberische populatie weinig minder dan die van de Canadees-Groenlandse. Dit toont aan dat het nadeel van een lange trekroute wordt gecompenseerd door overwinteren in een gunstige omgeving.

Verder zijn er verschillen in het ruiproces. Bij de eerstejaars Siberische vogels ruit 32% gedeeltelijk de vleugelveren; de Canadees-Groenlandse eerstejaars ruien niet. De duur van de rui van de handpennen van ouderejaars vogels was 45 dagen langer dan die van de Canadees-Groenlandse vo-

gels (119 resp. 74 dagen). De rui begon twee maanden later en verliep minder synchron. De Canadees-Groenlandse populatie beëindigde de hele zomer/herfst-rui voor het begin van de winterkoude.

Deze studie naar de verschillen tussen de jaarcyclus van de verschillende populaties brengt de onderzoekers niet dichtter bij een verklaring voor grote geografische verschillen die bestaan tussen de overwinteringsgebieden van de diverse Steenloper-populaties op de wereld.

HWdN

authors' addresses:

<sup>1</sup>353 Arbroath Road, Dundee, Scotland. <sup>2</sup>Department of Mathematical Statistics, University of Cape Town, Rondebosch, South Africa, 7700. <sup>3</sup>Department of Nature Conservation and Tourism, Windhoek, Namibia. Present address: Transvaal Department of Nature Conservation, Private Bag X211, Pretoria, South Africa, 0001.

<sup>4</sup>Dundee Museum, Dundee, Scotland.