Reproduction and Survival in a Declining Population of the Southern Dunlin *Calidris alpina schinzii*

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Reproductive success and survival was studied in a declining population of the Southern Dunlin in SW Skåne, S Sweden, in 1981-1986. Hatching success was low; on average only 30% of clutches hatched, due to intense nest-predation from mainly Crows, Foxes and mustelids. Some nests (8%) were also lost by trampling from grazing animals. Within a season, there was no significant difference in hatching success between early and late clutches, but the overall annual hatching success was higher in years with an early onset of breeding. On average, the Dunlins yearly produced 0.3 - 0.4 hatched young/adult. Fledging success was estimated at 36% and survival from fledging to the age of one year at 56%. Adult survival, estimated from return rates, averaged 89% in males and 77% in females (83% of the sexes combined). The sex-related difference in return-rates believed to reflect a lower actual survival rate in females, as suggested by the male-skewed sex-ratio in the population. The average life expectancy for an adult Dunlin is estimated at 5.4 years and the mean longevity at 7.4 years. Survival tended to decrease with increasing age (up to 5 years after ringing). The oldest bird recorded in the study was 17 years old. The observed reproductive rate was found to be insufficient to maintain a stable population and unless nest-predation is significantly reduced, the Dunlin will become extinct in SW Skåne within 20 to 30 years.

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Introduction

On the south-eastern edge of its distribution, along the coast of the Baltic and the North Sea, the Southern Dunlin *Calidris alpina schinzii* has decreased markedly in numbers during the past 50 years (Gromadzka 1983, Cramp & Simmons 1983, Piersma 1986). The main reason for this decline is believed to be the rapidly diminishing areas of suitable breeding habitat, *i.e.* wet meadows and pastures, grazed by domestic animals, or otherwise harvested by man (Larsson 1969, Dybbro & Jørgensen 1971, Soikkeli & Salo 1979, Emanuelsson & Kjellén 1981, Hansen 1985, Tjernberg 1985, Król 1986).

In this paper I present the results of a six-year study on a declining population of the Southern Dunlin in SW Skåne, South Sweden. Data on reproductive rate and survival are presented, and the possible factors controlling the population parameters and maintenance of the population are discussed.

Study area and methods

The study was performed in the years 1981-86, on the coastal wet meadows of SW Skåne, South Sweden (Figure 1). During the study period, these meadows held the bulk of the Swedish *schinzii*-population; 60-80 pairs out of an estimated total of about 250 pairs (Tjernberg 1985). Due to altered management (abolished grazing and hay-cutting) and exploitation (expansion of urban and industrial areas) of wet meadows, suitable breeding habitats for Dunlins and other waders have become scarce and fragmented in the whole of South Sweden (Emanuelsson & Kjellén 1981, Tjernberg 1985). The total area of typical Dunlin-habitat in SW Skåne is, at the time of writing, less than 300 ha, most of which is situated around the shallow Foteviken Bay (about 55°17'N, 12°58'E).

The main study area, Vellinge ängar (South), is located on the eastern shore of Foteviken Bay (Figures 1 and 2) and is comprised of approx. 60 ha of wet, intensively grazed shore meadow.

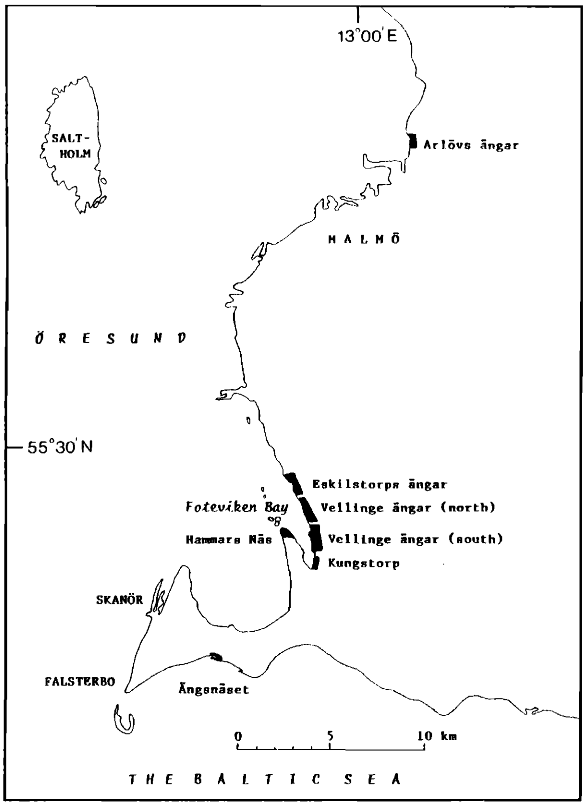

Figure 1. Location of the study areas (in black) on the coast of SW Skåne, South Sweden.

This locality still holds one of the largest concentrations of breeding Dunlins in Sweden (15-25 pairs during the study period). The area is separated from the northern part of Vellinge ängar by a ditch and a small (140 x 80 m) tree plantation. However, grazing animals can move freely over the whole area, totalling almost 120 ha. The meadows are grazed annually, from late May to well into October, by 150-250 cattle and 50-80 riding horses. A further description of the area is given in Jönsson (1985).

The control areas consisted of the remaining Dunlin localities in SW Skåne (Table 1), most of which are located within 4 km of the main study area; although two localities, Ängsnäset and Arlövs, are more distant (8 and 22 km, respectively) (Figure 1). The Danish island of Saltholm, which in 1980 held up to 15 pairs of Dunlin (Hansen 1985), is situated 25 km NW of Vellinge ängar, but was for practical reasons not included in this study.

Table 1. Mean population size and density of breeding Dunlins in SW Skåne, 1981-1986.

Locality	Area (ha)	Number of pairs	Maximum breeding density (pairs/ha)
Main study area			
Vellinge ängar (S)	60	14-24	0.40
Control areas			
Vellinge ängar (N)	58	15-20	0.35
Eskilstorps ängar	55	10-25	0.46
Kungstorp	9	1-2	0.22
Hammars Näs	33	3-5	0.15
Arlövs ängar	44	3-4	0.09
Ängsnäset	10	1-2	0.20

In the main study area, my aim was to capture and mark as many birds as possible, and to find all nests in every season. The main objectives of the visits to the control areas were to estimate the number of breeding birds and to check for and identify marked individuals, however, I also ringed a few adults and chicks. In 1983-1985, the main study area was expanded to include also Vellinge ängar (North) and Ängsnäset.

Nests were searched for by careful investigations of suitable parts of meadows, and by

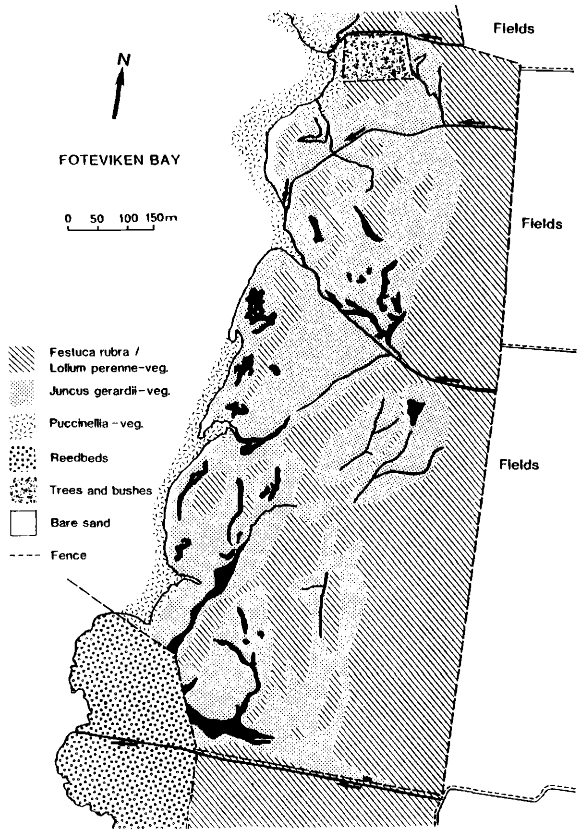

Figure 2. Map of the main study area, Vellinge ängar (S), showing the distribution of some important vegetation types.

watching the behaviour of the birds. During the first period of egg-laying, from mid-April until mid-May, nests were relatively easy to find just by searching on the dry spots with low vegetation; *i.e.* the only places where it was possible for the birds to lay their eggs at that time. Later in the season, with virtually the whole area dried up and with higher vegetation, nests were more difficult to find (see Jönsson 1985). On average I estimate that 75-95 % of all nests in the main study area, were found annually.

All nests and broods were plotted on a field map, and their fate subsequently recorded. The hatching date of incubated broods was estimated by immersing the eggs in water (see Westerskov (1950) and van Raasen *et al.* (1984). Nest losses were recorded as well as the probable causes for these losses (predation, trampling or desertion). In predated nests, signs of the predator were looked for.

Adult birds were caught on the nest during incubation, using walk-in-traps (see Bub 1974), while chicks were caught by hand, as soon as possible after hatching.

All birds caught were ringed with one metal-ring and 2-5 coloured plastic rings. A unique combination of colour-rings was used for each single individual. Table 2 gives the annual numbers of ringed birds in the main study area and the control areas.

Sex, in adult birds, was determined from plumage characters and measurements, in combination with subsequent behavioural observations (see Soikkeli 1973, Ferns & Green 1979 and Jönsson 1987).

On every visit to the study areas, colour-ringed birds were looked for and, if possible, identified using binoculars (10x40) and a telescope (20-40 x 60). With favourable light conditions, colour-rings could be read accurately at a distance of 150 to 200 meters, using the 40x magnification ocular on the telescope.

Results

Nesting success

The frequency of clutches that survived until hatching, varied between years from 16% in 1983, to 38% in 1984, averaging 30% for the whole study period (Table 3).

Thus, a large majority of the clutches laid each year were destroyed or deserted. The most important factor affecting nest survival is predation. In total, 60% of all clutches were taken, completely or partially, by predators. In most cases no sign of the predator was found, but sometimes egg-shell fragments showed the characteristic marks of Crows *Corvus corone* or small Mustelids (most probably Stoat *Mustela erminea*). Another important predator on Dunlin eggs was probably the Red Fox *Vulpes vulpes*, which was seen regularly patrolling the meadows for waders' nests (see also Jönsson 1985).

Partial predation, *i.e.*, where just one or two

Table 2. The annual numbers of Dunlins trapped and ringed in the main study area and the control areas. Left figure = adults, right figure = young.

	1981	1982	1983	1984	1985	1986
Vellinge ängar (S)	43/31	14/18	9/3	1/6	5/6	1/-
Vellinge ängar (N)	-/-	1/-	15/7	23/28	10/25	3/3
Eskilstorps	-/-	-/-	2/7	-/-	-/-	-/-
Kungstorp	-/-	-/-	-/-	-/-	-/-	3/-
Hammars näs	-/-	-/-	-/-	-/-	-/-	-/-
Arlövs ängar	-/-	1/3	1/-	-/-	2/2	1/-
Ängsnäset	-/-	2/4	1/4	-/-	-/-	-/-
Total	43/31	18/25	28/21	24/34	17/33	8/3

Table 3. Nesting success in a Dunlin population in SW Skåne in 1981-1986. Figures refer to clutches.

	Hatched		**Predated**		**Trampled**		**Deserted**		**Total**	
	n	**(%)**	**n**	**(%)**	**n**	**(%)**	**n**	**(%)**	**n**	**(%)**
1981	13	(36.1)	20	(55.5)	2	(5.6)	1	(2.8)	36	(100)
1982	8	(28.5)	18	(64.3)	1	(3.6)	1	(3.6)	28	(100)
1983	6	(16.2)	26	(70.3)	4	(10.8)	1	(2.7)	37	(100)
1984	12	(37.5)	18	(56.2)	2	(6.3)	0	(0)	32	(100)
1985	12	(29.3)	21	(51.2)	7	(17.1)	1	(2.4)	41	(100)
1986	9	(31.0)	19	(65.5)	0	(0)	1	(3.5)	29	(100)
Total	60	(29.6)	122	(60.0)	16	(7.9)	5	(2.5)	203	(100)

eggs were taken from the clutch, accounted for nearly 7% of the nest losses. Generally the birds abandoned the remaining eggs after a partial predation had occured, but in two cases incubation continued and the reduced clutches hatched normally.

The seasonal changes in nest survival, with regard to predation, are expressed as daily survival rates according to the method developed by Mayfield (1961, 1975) and Johnson (1979). Daily survival rate may be defined as the probabilty, P, that a nest present one day would survive to the next day. It is estimated from the formula:

$$P = A/(A+B)$$

where A = total number of 'nest days' (the sum of all daily totals of nests present during the observation period), and B is the total number of nests lost. The day on which a nest was lost is not counted as a nest day and nests were assumed to have been lost half way between the last two checks. Data were grouped weekly during the nesting period and P-values given for each week are presented in Figure 3. The pattern emerging showed a high survival rate during week 1 (15-20 April), with virtually no losses, then a marked decrease during week 2 and 3, with P falling to 0.94. During weeks 4-6 (6-26 May), the daily survival rate was rather stable, around 0.97, but dropped to a clearly lower level (0.92) in week 7 (27 May-2 June). The variation found in daily survival rate (P), is significantly different from that expected with an equal rate over the whole nesting period (Chi^2 = 26.9, $p<0.001$, df = 7). Excluding data from week 7, there is still an almost significant (Chi^2 = 11.3, $0.1>p>0.05$, df = 6) difference between the observed survival rates and those expected with an equal survival rate over the whole period. This period of increased nest predation coincided with the annual release of the grazing herds of cattle and horses, in the last days of May (Jönssen 1985).

Losses due to trampling by grazing animals represented a minor part, only 11%, of the total nest losses (Table 3). However, in single years, *e.g.* 1985, trampling may destroy many clutches. I have no data to separate trampling by cattle from that by horses, but experience from other

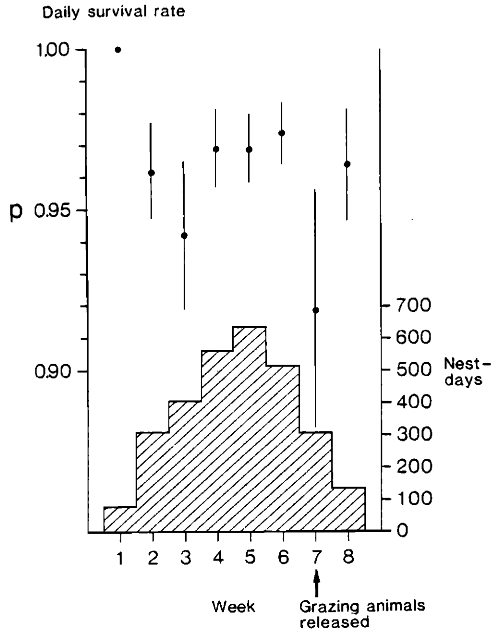

Figure 3. Daily survival rates of Dunlins' nests and eggs in different weeks, during egg laying and incubation. P-values (dots) are calculated for losses by predation only and given within 95% confidence intervals. Hatched columns = number of nest days per week.

meadows in SW Skåne indicates that horses, due to their more lively behaviour (especially when in large groups), cause more trampling losses than cattle (Andell & Jönsson 1986).

In the rather few cases where whole clutches have been deserted, it is likely that one of the parent birds have died.

Hatching success

Hatching success measured as the frequency of hatched clutches, was on average 29.6% (Table 3). Comparing first clutches with replacement and second clutches, the frequency of successful clutches was 26.9% (n = 1982) and 32.4 (n = 34), respectively. The difference was not statistically significant ($Chi^2 = 0.43$, $p<0.5$, df = 1). Neither was there any significant difference in hatching success between early and late clutches; hatching frequency being 26.0% for clutches commenced before the 5th of May (median date for start of egg-laying in all clutches), and 27.6% for clutches laid after this date (Chi^2 = 0.0.2, $p<0.8$, df = 1).

The proportion of eggs laid that hatched, varied between 15.5 % in 1983 (n = 103) and 28.6 % in 1985 (n = 91), with an overall total of 23.7 % for the years 1981-1985 (n = 514). In clutches which were closely inspected during hatching, 116 eggs (94 %) hatched normally, while 8 eggs (6%) were either infertile (n = 6) or deserted before the chick was hatched (n = 2).

Measuring hatching success as the number of chicks hatched per adult bird shows that the population in the main study area produced on average 0.34 young per adult and year. Including data from two of the control areas (Vellinge ängar N and Ängsnäset), which were thoroughly investigated in 1983-1985, the overall hatching success was 0.40 young per adult (Table 4).

Fledging success

Due to the cryptic colouration and elusive behaviour, Dunlin chicks are very difficult to find and observe after they have left the nest (see also Heldt 1966, Holmes 1966, Soikkeli 1967). Furthermore, the young normally left the breeding area very soon after fledging, making a direct control of fledging success impossible. To get an estimate of fledging success, I used an indirect method, on the basis of the return rate of birds ringed as chicks and later controlled in the study area. During the years 1981-1985, a total of 144 chicks were ringed. Out of these, 24 (16.7 %) were controlled 1-5 years later (Table 5). The number of birds alive one year after hatching, N_1, may be calculated according to the formula of Soikkeli (1970a):

$$N_1 = \sum_{x=1}^{\infty} n_x (100/S)^{x-1} \qquad (1)$$

where n_x is the number of birds found for the first time when x years old, and S is the mean annual survival rate after the age of one year. Using the data in the right-hand column of Table 5, and assuming that S during the second year of life is the same as during later years, *i.e.* 83 %, then N_1 = 29, or 20.1 % of the ringed chicks.

Each year, a smaller number of independent fledglings are observed before departure. In the years 1981-1985, 18, or 12.5 %, of the ringed chicks were seen as fledglings, whereas 8 (44.4%) were recovered in later years. The total number of ringed fledglings, N_f, may be calculated from the following equations:

$$N_f = N_1 \left(\frac{n_{fo}}{N_{1fo}}\right) \qquad (2)$$

where n_{fo} is the number of observed fledglings, and N_{1fo} the number of observed fledglings

Table 4. Hatching success in a Dunlin population in SW Skåne in 1981-1986. 1 = main study area, 2 = main study area + control areas Vellinge ängar (N) and Ängsnäset (cf. Fig.ure 1)

	Adults present		Successful nests		Young hatched		Young per adult	
	1	2	1	2	1	2	1	2
1981	50	-	14	-	40	-	0.80	-
1982	47	-	6	-	18	-	0.38	-
1983	47	86	2	6	4	17	0.09	0.20
1984	37	77	3	13	10	35	0.27	0.46
1985	35	75	3	11	9	34	0.26	0.45
1986	38	-	2	-	6	-	0.16	-
Total	254	373	30	52	87	150	0.34	0.40

alive after one year. We know from above that $N_1 = 29$ and $n_{fo} = 18$. As with N_1, we get from equation 1 that $N_{1fo} = 10$. Thus, $N_f = 52.2$, which gives us an estimated fledging success of 36.3 % (= 52.2/144).

To use this method for calculating fledging success I also assume that survival in the first year is the same for those fledglings actually observed, as for those not observed. At present, there is no reason to believe that this should not be the case.

A possible source of error, which may result in a too high estimate of fledgling success, is that some broods may succumb before the chicks are ringed. However, during the years 1981-1986, I have only registered three such cases where the newly-hatched broods were killed by predators before ringing and if these chicks were included in the analysis, estimated fledging success would be modified to a small extent only, to 33.5 %. A more serious source of error may affect my estimate of fledging success if the return rate of first-breeding birds is significantly lower than the actual rate of survival. It is reasonable to believe that some of the young disperse to breeding sites outside the study area. However, since nearly all the suitable breeding areas in the region were checked for ringed birds annually, the number of live birds missed must be limited. This is supported by the fact that Soikkeli (1970b) in Finland found no case of first breeding Dunlins having dispersed outside a radius of 5.0 km from the birthplace.

The reasons for chick mortality during the fledging period are not known in detail, but I am sure that many young are taken by predators, primarily Crows and Red Foxes. Small chicks (less than a week old) are also vulnerable to longer periods of cold and wet weather, when food availability is reduced and permanent brooding by the parents is needed to maintain the body temperature. A few chicks probably also die each year due to trampling by grazing animals.

First-year survival

An estimate of the post-fledging survival of the first year of life was obtained from the return rate of birds ringed as chicks. Following the calculations made above (see under 'Fledging success'), assuming that the birds observed as fledglings are representative for all young, first-year survival was estimated at 55.6 % (N_{1fo}/N_{fo} x 100). Most birds were recovered when two years old (Table 5), which is the age at which they usually breed for the first time (Heldt 1966, Soikkeli 1967). Breeding by first-year birds was only confirmed in three cases (all females), although some young males established territories each year and tried to attract females.

Among the 24 birds ringed as chicks and later recovered in the study area, 17 were males and only 7 females. The difference is close to statistically significant (p = 0.06, two-tailed binomial test).

Table 5. Age when recovered for the first time and survival up to the age of one year in Dunlins ringed as chicks in SW Skåne in 1981-1985. M=males, F=females.

	Year of ringing					
Age when first recovered	**1981 M+F**	**1982 M+F**	**1983 M+F**	**1984 M+F**	**1985 M+F**	**Total M+F**
1	2+1	0+0	0+0	0+0	4+0	6+1
2	4+0	2+1	1+1	2+2	- -	9+4
3	0+0	1+0	1+0	- -	- -	2+0
4	0+1	0+0	- -	- -	- -	0+1
5	0+1	- -	- -	- -	- -	0+1
Tot. recov.	6+3	3+1	2+1	2+2	4+0	17+7
No. ringed	31	25	21	34	33	144
Surv. 1 year (N1)	11	1	4	5	4	29
Surv. 1 year (%)	35.5	20	19.1	14.7	12.1	20.1

Table 6. Annual return rates of adult Dunlins in SW Skåne 1981-1986.

	Males			Females			
	Individuals present in previous year	Individuals returning following year	Return rate	Individuals present in previous year	Individuals returning following year	Return rate	Total return rate
1981-1982	24	22	0.92	24	18	0.75	0.83
1982-1983	35	31	0.89	29	26	0.90	0.89
1983-1984	44	38	0.86	42	34	0.81	0.84
1984-1985	52	45	0.87	46	33	0.72	0.80
1985-1986	56	52	0.83	44	31	0.71	0.83
Total	211	188	0.89	185	142	0.77	0.83

First year survival of early-born chicks (hatched before 31 May) did not differ from that of late-born chicks (hatched after 31 May); the return rate of young hatched early in the season was 16.7 % (n ringed = 84), as compared with 17 % for late-born ones (n ringed = 59).

Adult survival

Adult survival was estimated from the return rate to the study area of ringed breeding birds. As in all migratory birds, the reliability of survival rates derived from return rates depends on the site tenacity of the birds. In the Southern Dunlin, males are known to be very faithful to their breeding area and return year after year to the same territory (Soikkeli 1967, 1970b). Thus, non-returning adult males can with great certainity be regarded as dead. Female survival is more difficult to estimate since they disperse between breeding season to a higher degree than males (Soikkeli 1970b, own observations). However, since this study covered most of the suitable Dunlin localities within a radius of 100 km, the number of females dispersing outside the area, are probably very few. Annual return rates may therefore be regarded as good minimum estimates of survival in adult Dunlins.

The overall annual return rate of adult Dunlins in SW Skåne, was 83 %, varying between 80 % in 1984/85 and 89 % in 1982/83 (Table 6). The average male return rate (89 %) was significantly higher than that for females (77 %) ($Chi^2 = 12.1$, $p<0.001$, df = 1). Only in one year (1982/83) was the return rate higher in females than in males: 90 % vs. 89 %.

In both males and females, the annual return rate tends to decrease with increasing age (Table 7). When expressed as a linear regression (Figure 4), this relationship was statistically significant in both males ($r = -0.86$, $p<0.02$, $n = 5$) and females ($r = -0.95$, $p<0.01$, $n = 5$). However, when using a Chi^2-test and, comparing the observed proportions of returning birds with those expected from a null-hypothesis (predicting no difference in return rate with increasing age), no significant differences were found: $Chi^2 = 4.15$, $p>0.20$, df = 3 (males) and $Chi^2 = 4.20$, $p>0.20$, df = 3 (females).

Most of the adult mortality is believed to occur during the non-breeding season, *i.e.*, on migration, or on the wintering grounds (see Soikkeli

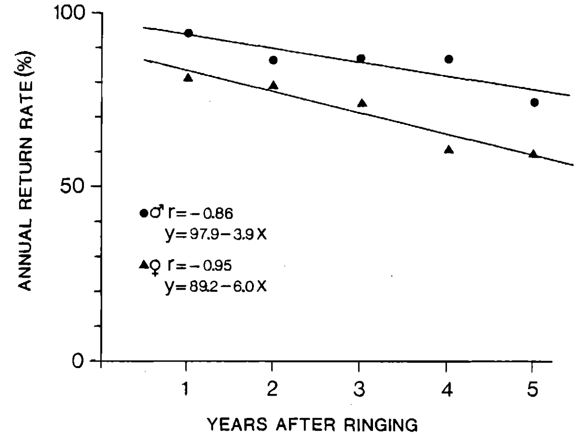

Figure 4. Return rates of adult Dunlins in relation to increasing age. See text for discussion about statistical significance.

Table 7. Return rate of adult Dunlins in relation to increasing age in the population of SW Skåne 1981-1986. M = males, F=females.

	individuals present in previous year			individuals returning following year			% returning		
Years after ringing	M	F	M+F	M	F	M+F	M	F	M+F
1	75	74	149	71	60	131	95	81	88
2	60	52	112	52	41	93	87	79	83
3	40	36	76	35	27	62	88	75	82
4	24	18	42	21	11	32	88	61	76
5	12	5	17	9	3	12	75	60	71

1967, Evans & Pienkowski 1984). In this study, only two birds were definitively known to have died in the breeding area. These were both males taken by avian predators (a Merlin *Falco columbarius* and a Sparrowhawk *Accipiter nisus*, respectively) during the prelaying period, early in the season. However, at least two more birds (both females) disappeared during the incubation period, probably taken by some mammalian predator at night while incubating the eggs.

Life expectancy and longevity

With a constant annual mortality rate M (in %, = 100 x annual survival rate), the average expectation of life is 100/M-0.5 years. With an average annual mortality rate for adults of 17 % (Table 6), life expectancy was calculated as 100/17-0.5, or 5.4 years. Separating the sexes, mean life expectancy for males was 8.6. years (M = 11 %), and for females 3.9 years (M = 23 %).

These values of life expectancy, were used to calculate an estimated mean longevity for adult Dunlins in two ways: 1. Assuming that most of the adults are breeding for the first time when caught and ringed, we need only to know the mean age of first-breeders and then add life expectancy to obtain mean longevity. The mean age of 9 first-breeders, ringed as chicks and controlled breeding in later years, was 2.0 ± 0.36 years. Thus, mean longevity for adult birds will be 7.4 years (sexes combined). Assuming further that there is no difference in the mean age of first-breeding males and females, mean longevity for males will be 10.6 years and for females 5.9 years. 2. Mean longevity can be derived also from calculations using only birds of known age, *i.e.*, birds ringed as chicks and later controlled in the study area. During the study period 24 such Dunlins were controlled. Seven of these have since disappeared and are considered dead. The total age of the dead birds amounted to 13.5 years, assuming equal mortallity rate in the first and second halves of the year. The remaining 17 birds still alive in 1986, had a total age of 49 years and their additional total life expectancy was 17 x 5.4, or 91.8 years. The mean logevity of these 24 Dunlins would thus be (13.5 + 49 + 91.8)/24, or 6.4. years. Similar calculations for males (n = 17) and females (n = 7), give mean longevity values of 9.1 years and 5.1 years, respectively.

Mean longevity of young Dunlins, hatched or fledged, is of course much shorter than that of breeding birds.

In the study population there were at least four birds attaining an age of 14 years, and another that reached 7 to 11 years. These birds were all, with one exception, ringed as newly fledged juveniles near Falsterbo in southernmost Skåne (*cf.* Figure 1). The two oldest ringed birds, both males, aged 17 and 16 years, respectively, were still alive in 1987 (pers. obs.).

Discussion

Reproductive success

From the results presented above, it is clear that reproductive success for Dunlins in SW Skåne is severely limited by nest predation. The over-

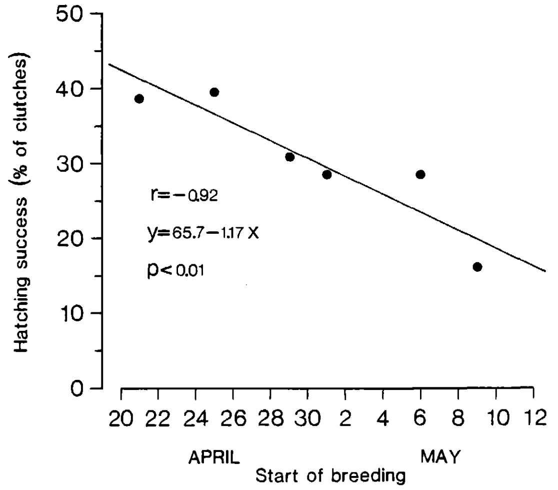

Figure 5. Hatching success of Dunlins' nests in SW Skåne in 1981-1986, in relation to the annual median date for start of egg-laying of first clutches.

all hatching success of about 30 % is less than in any other Dunlin population studied (Holmes 1966, Soikkeli 1970a, Etheridge 1982, Król 1985), but comparable to the low values reported for British Redshanks *Tringa totanus* (Hale 1980) and Ringed Plovers *Charadrius hiaticula* (Pienkowski 1984). Generally, nest predation tends to be higher for waders breeding in temperate areas, as compared with those breeding in arctic regions (Jehl 1971, Evans & Pienkowski 1984).

As seen from Figure 3, nest survival varied somewhat during the season, with two distinct 'dips' in week 3 and 7, respectively. The significantly higher predation rate in week 7 is probably related to the annual release of the grazing animals in the study area. During the first few days after the release, the herds of cattle and horses behave very uneasily, running back and forth over the meadows. This disturbs the incubating waders, which frequently are chased off their nests. Predators, especially Crows, probably take advantage of the general disorder in the meadows during these days, having an easy time finding the nests by observing the anxious waders flying around.

The first period of higher nest predation in week 3 is more difficult to explain, but may reflect the predators' response to the sudden increase in an easily availabe food resource in the form of waders' eggs. The following period of relatively high and stable survival rate in weeks 4-6, may be a consequence of more alternative food resources now being available for the predators.

As mentioned earlier, there was no difference in hatching success between early and late clutches. In other wader species hatching success was found to be low early in the season, due to a high predation rate (Byrkjedal 1980, Meltofte *et al.* 1981, Pienkowski 1984). Neither was there any tendency for higher fledging success in early, as compared to late, clutches, as found by Soikkeli (1967) in a Dunlin population in SW Finland. However, the overall annual hatching success was inversely correlated with the median date for start of egg-laying in the years 1981-1986 (Figure 5). Since hatching success is very much dependent on the intensity of nest predation, this relationship indicates a higher predation rate in years with a late start of breeding. The reason for this is not obvious, but it is possible that late years, with cold and rainy weather, are generally poor in other food resources for predators like crows and foxes, subjecting wader eggs to a higher predation pressure.

Survival in relation to age and sex

The lower survival of first year birds (56 %), as compared to older birds (83 %), is consistent with the general pattern in waders and most other birds (Perrins & Birkhead 1983, Evans & Pienkowski 1984). This was also the conclusion made by Boyd (1962), although his estimates, mostly derived from recoveries by the public of ringed birds, were at much lower levels for many species.

My estimate of a first-year survival of 56 % in the Dunlin is in close agreement with the values given for Oystercatcher *Haematopus ostralegus* (69 %) by Harris (1967), Curlew *Numenius arquata* (50 %) by Bainbridge and Minton (1978), and Ringed Plover (59 %) by Pienkowski (1984).

In a study of wintering Dunlin *C.a. pacifica* in California, Kus *et al.* (1984) found that Merlins and other avian predators killed a higher proportion of juveniles than expected from their actual frequency. High mortality among first-year birds is generally thought to be the result of their relative inexperience in dealing with different selective agents, such as predation, feeding efficiency and extreme environmental conditions (Goss-Custard 1980, Evans & Pienkowski 1984).

The data collected in this study does not allow any estimate of second-year survival, but according to what is known from other species, it is not significantly different from that of older birds (Evans & Pienkowski 1984).

In adult birds, survival is generally considered to be constant and independent of age (Perrins and Birkhead 1983). This was also the conclusion by Soikkeli (1970a) about the Dunlin population in Finland. However, in this study return rates indicate a decreased survival with increasing age (Table 7, Figure 4), and Hildén (1978) found a similar tendency in his population of Temminck's Stint *Calidris temminckii.* Using the method of Hildén (1978) and calculating a linear regression of return rates in relation to age after ringing, revealed significant inverse correlations for both sexes (Figure 4). However, testing the differences in return rate between different years after ringing, with a Chi^2-test, these were not statistically significant. A similar test made on Hildén's (1978) data, also failed to establish any significant decrease in return rate with increasing age (Chi^2 = 8.20, $0.1 \leq p \leq 0.05$, df = 4). These conflicting results make it difficult to draw any definite conclusions about the effect of age on the survival of adult waders. However, I agree with Hildén (1978), citing Botkin & Miller (1974) and Coulson & Wooler (1976), that age-dependent survival is likely to occur in such long-lived species.

The pronounced difference in return rate between males and females, as found in this study, (see Table 6) has not been reported for any other monogamous wader species or population. Soikkeli (1970a) in his study of Dunlins in Finland, found no significant sexual differences in return rate (77 % in males and 72 % in females). The average return rate for males in Finland was also significantly lower than that found in this study (Chi^2 = 10.0, $p<0.01$, df = 1). Miller (1983), in a study of the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia, reported a return rate for males of 65 % and for females 38 %. However, these values were based on records from only two successive years.

Generally, sexual differences in return rate of waders are small, although in most cases, males tend to show the highest values (Oring & Lank 1984). The obvious question to ask is of course if these sexual differences actually refer to a higher survival in males, or if they reflect the higher dispersal rate of the females, which is well documented in many species (Soikkeli 1970b, Oring & Lank 1984, pers. obs.).

In the present case, I have reason to believe that the observed difference in return rate between the sexes is not solely the result of differential dispersal. Besides the relatively high efficiency in searching for ringed birds, with nearly all suitable Dunlin localities in the surrounding region controlled each year, there are two facts supporting a genuine difference in survival between the sexes:

1. Among the ringed birds recorded as missing (not observed) in one year, some are recovered alive in a later year. The frequency of such 'missed' birds is not higher for females (18.9 %, n = 53) than for males (17.9 %, n = 28), which would be expected if dispersal was the major reason for the lower female return rate.

2. Furthermore, the constant and clearly skewed sex-ratio in the breeding population at the main study area (Table 8), would not persist if there was no difference in survival rate between the sexes.

Table 8. The operational sex-ratio in a Dunlin-population in SW Skåne in 1981-1986. Data from the main study area.

	No. of males	No. of females	Ratio males:females
1981	26	24	1.08:1
1982	25	22	1.14:1
1983	25	22	1.14:1
1984	22	15	1.47:1
1985	21	14	1.50:1
1986	22	16	1.38:1
mean	24	19	1.29:1

There was a clear tendency that more males than females return as first-breeders to their birth-place, as seen from Table 5. Soikkeli (1970b) found no significant sex-difference (30 males, 27 females) among returning young ringed as chicks, and similarly equal sex-ratio among first-breeders are found in most other wader species studied (Oring & Lank 1984). The only case indicating a more distinct sex-bias in natal philopatry or juvenile survival is that of the Long-billed Curlew *Numenius americanus* in SW Idaho, reported by Redmond & Jenni (1982), where 9 males and two females were recovered on their natal breeding grounds.

In adults, the lower annual survival rate of females may be related to the cost of reproduction. The laying of one or two four-egg clutches, each one weighing 80-90 % of the female's own weight, is probably a great energetic strain and it has been demonstrated that females of different *Calidris*-species loose weight rapidly during the whole incubation period and the early brood-rearing period (Ashkenazie & Safriel 1979, Erckmann 1981, Jönsson & Alerstam 1990). This indicates that females are exposed to a more serious energetic stress, just after the breeding season, which might lead to an increased mortality during the following migration to the moulting areas (*e.g.* the Southern Dunlin).

Another explanation for the relatively low survival of females could be that they, due to their larger size, are more vulnerable to aerial predators like Merlins and Sparrowhawks. The selective advantage of small size for flight agility, avoiding a predator and making quick turns, has been emphasized by many authors (*e.g.* Andersson & Norberg 1981, Jehl & Murray 1986).

Maintenance of the population

As already indicated by the high nest-predation, the yearly reproductive output in the studied population is low; on average 0.13-0.15 fledged young per adult. In comparison, the Dunlin population studied by Soikkeli (1967, 1970) in SW Finland, produced on average 0.26 fledged young per adult and year, assuming that the fledging rate in Finland was the same as in this study (36.3 %). As a further comparison, Hildén (1978) reported an average fledging rate of about 0.7 young per adult in a population of Temminck's Stint.

Is then the recorded reproductive rate sufficient to balance the annual mortality rate? Is the population self-supporting? As about 17 % of the adults die annually, the proportion of first-breeders should also be 17 %, which means that the population must produce 0.17 first-breeders per year and adult. With an annual fledging rate of about 0.14 young and a post-fledging survival rate of about 56 %. then 0.14 x 0.56 = 0.08 young reach the age of one year. Using the data in Table 6, we can estimate the proportions of birds breeding when one and two years old, at 35 % and 65 %, respectively. If the survival rate during the second year of life is the same as for adults, *i.e.* 83 %, then the number of first-breeders produced per adult = 0.08 (0.35 + 0.65 x 0.83) = 0.07. Thus, the reproductive output of the population is far below the 0.17 first-breeders needed to keep it self-supported. The low hatching success is the main factor responsible for the insufficient reproductive rate. To balance the adult mortality, hatching success in the study area must be increased from the prevailing 0.34-0.40, to about 1.0 young per adult and year.

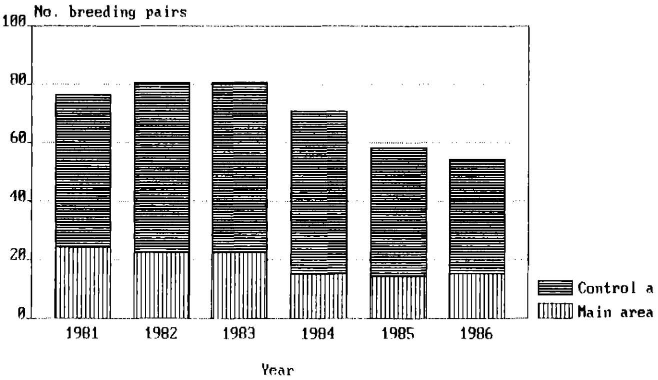

Figure 6. Development of the Dunlin population in SW Skåne in the years 1981 to 1986.

Provided that immigration and emigration balances, the recorded values of mortality and reproductive output should bring, as a consequence, an annual decrease of the population in the order of 10 %. As seen from Figure 6, the actual decrease during the six-year period, has been around 5 % per year. This indicates that there is an annual immigration rate of about 5 %, which partly compensates for the low internal reproduction. However, since the Southern Dunlin is reported to be decreasing in all countries around the Baltic Sea (Gromadzka 1983, Hansen 1985, Tjernberg 1985, Klafs and Stübs 1987), the external support to the population in SW Skåne is not likely to persist for any extended period of time. With no radical improvements in the reproductive success, the Dunlin population of SW Skåne will slowly meet the fate of extinction a decade or so, into the next century.

The role of nest-predation as a regulating factor for birds, like the Dunlin, breeding in wet meadows has become evident in South Sweden in recent years, especially following the outbreak of sarcoptic mange in Red Foxes (Lindström 1987). Significantly increased hatching success has been reported for *e.g.* Dunlins (Jönsson 1990) and Lapwings (Flodin *et al.* 1990) in areas where the foxes have disappeared. Continuing area decrease and the fragmentation of well-managed wet meadows may also increase the impact of nest-predators on wader populations breeding in these habitats (Jönsson 1990).

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