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Survival prospects of single-brooded and double-brooded Rock Pipits *Anthus petrosus*

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In a small, colour-ringed population of migratory Rock Pipits in the Gulf of Finland, no apparent impairment in survival prospects emerged among yearlings that bred twice in their debut breeding (double-brooded) compared with those that only bred once (single-brooded). Of the several variables measured, only timing of breeding differed between single- and double-brooded individuals: single-brooded birds bred about two weeks later than double-brooded birds. However, the occurrence of double-broodedness increased with increasing age. The frequency of double-broodedness was lowest in years when winters were harsh in NW Europe. Hence, depending on the timing of spring, many Rock Pipits may start their breeding career prudently as single-brooded but turn double-brooded in subsequent years. Reproducing once or twice in a season seems to be a joint product of age-dependent breeding schedule and concurrent environmental constraints.

1. Introduction

In northwestern Europe, the Rock Pipit *(Anthus petrosus)* is the most maritime of land-birds, predominantly inhabiting woodless rocks and skerries in the outermost archipelago (Cramp 1988, von Numers 1995). Being highly tolerant of extreme conditions, the species arrives early in spring and departs late in autumn; in the northern Baltic, it stays longer at the breeding site than any other archipelago bird (own obs.). The long breeding period extends from late April to early August, during which time a considerable proportion of females nest twice, i.e. double-brooded (e.g. Hario 1982, Askenmo & Unger 1986).

The current life history theory postulates the cost of reproduction, although empirical studies readily fail to quantify the trade-off between current and future reproduction in birds (for reviews, see Lindén & Møller 1989, Newton 1989, Partridge 1989, Lessels 1991). Double-broodedness is among the traits for which costs in the form of lower parental survival have been demonstrated in a correlational study (Bryant 1979).

In this paper I will report the breeding lifespan of single-brooded vs. double-brooded Rock Pipits in a small, colour-ringed population. I will report whether there are differences in life expectancy between individuals that choose to make one vs. two broods in their debut year, and whether there are phenotypic traits predicting the occurrence of single-broodedness vs. double-broodedness in Rock Pipits. I did not take into account the postulated reproductive costs arising from different breeding strategies.

2. Material and methods

The study was carried out at the Söderskär bird sanctuary, an isolated archipelago of c. 25 small islands in the central Gulf of Finland (60°07´N, 25°25´E). The area holds one of the densest Rock Pipit populations in Finland (Hildén & Hario 1993).

During 1982–95, I colour-ringed a total of 60 individuals breeding on three small islands. The breeding lifespan was established for 27 females and 23 males which entered the population during 1983–92. None of these individuals survived to breed in 1995.

All unringed breeders recorded were assumed to be yearlings, and the survival was determined from the return rates to the study area. Hence, the actual age of the recruits was not known. This resulted mainly from the apparently high dispersal rate of the local offspring, as shown in many other studies on small passerines (see, e.g. Newton 1989, Lundberg & Alatalo 1992, Møller 1994). Out of 268 ringed fledglings, only two (males) returned to the natal site, turning up in their first year of life (and one paired with its mother).

As a measure of the lifetime reproductive output, I used the number of breeding attempts rather than the number of fledglings because the content of a nest could not always be investigated accurately, because of the inaccessibility of some nest sites.

The birds were sexed mainly on the basis of their behaviour, males being located and mist-netted while singing or displaying, and females when feeding the young; actually most nests were first located at the nestling stage. No nest predation, whatsoever, occurred on the islets, the Hooded Crows *(Corvus cornix)* being the only potential predators. In addition, their impact on nest losses on the man-inhabited islets was nil. Flooding due to heavy rain was the principal cause for some nesting failures observed.

Because I lived permanently on the islets all through the breeding season, I was able to check the colour combination of each individual soon upon its arrival in spring. I made daily observations of the territory occupation, displaying males being readily seen and heard from my yard (a lighthouse keeper's house) in this spectacularly open and rocky terrain. I find it most unlikely that any nesting attempt could have escaped my notice. Even though I often made the final nest search only after hatching (for pragmatic reasons), I had located and mapped the territories and identified the breeding pairs already during the courtship. There were three cases of bigamy and two successful renestings, results of which I have included in some of the data to preserve sample sizes (see later).

When caught for the first time, each bird was measured and weighed and its body fat assessed (indices of visible fat ranging from 0 to 6, Pettersson & Vuorinen 1984). To avoid the effect of wear on the primary and tail feather lengths, only the measurements from spring and early summer were used. Wing length was taken with Svensson's method 3 (1992; maximum length), and tail length with the "Operation Baltic" method (tail folded towards back; Busse & Kania 1970). Bill length was measured as the chord from bill tip to the skull, and tarsus length was taken from the tarsal joint to the middle toe joint (toes bent back, see Svensson 1992).

Timing of breeding was taken as the fledging date. In the statistical tests the effect of year has been controlled by expressing the date as a deviation (in days) from the median date of fledging of all known first broods in the data (25 June, n = 27).

The quality of the nest site (the nest cavity) was expressed as the number of times the site was used by Rock Pipits for a successful breeding. Nearly all nests were well hidden in rock crevices, in blast stone piles, under big stones or in stone fillings, some even in nest boxes and in buildings. Of the 54 successful nest sites, 38 (70%) were used only once, 10 were used twice (19%) and the remaining six were used three to five times each.

3. Results

3.1. Longevity and reproduction output

Site-tenacity among the established birds was high. Of the 60 colour-ringed individuals only one female moved to another islet (1 km apart) after having bred for two seasons on the study islands. From this I concluded that birds that disappeared had died and not moved elsewhere (see also Hötker 1988, 1989, Møller 1994). Furthermore, there were no instances of an established breeder disappearing one year and reappearing the next.

On average, an established Rock Pipit female lived 1.6 breeding seasons, producing 2.4 broods (Table 1). The distribution is strongly skewed towards first-year birds: 70% of all females lived only one breeding season producing 42% of all broods. For the males, the corresponding figures were 57% and 28%. The two females that lived the longest produced 31% of all broods. The mean number of broods in males includes three instances of verified bigamy; with them included, males lived on average 2.0 seasons producing 2.8 broods.

Most of the single broods were produced by yearlings (Table 1), and the occurrence of double-broodedness increased with increasing age. Therefore, a meaningful comparison of survival prospects between single-brooded and double-brooded birds is yearlings. The life-expectancy of single-brooded yearling females (mean 1.60 breeding seasons, SD 1.31, median 1, n = 16) was equal to that of double-brooded yearling females (mean 1.58, SD 1.29, median 1, n = 11; Mann-Whitney U-test, z = 0.106, P = 0.916). Double-brooded yearling males lived suggestively longer (mean 2.18, SD 1.40, median 2, n = 11) than single-brooded yearling males (1.64, SD 1.21, median 2, n = 11; z = 1.511, P = 0.131).

The mean annual return rate of breeding females was 0.49 (SD 0.30) and of males 0.51 (SD 0.36). Thus, the Rock Pipit seems to be a typical short-lived passerine with no more than half of the established breeders surviving to breed the next year.

3.2. Mean production and timing of the debut breeding

In an attempt to find features that would allow one to identify potential single-brooded vs. double-brooded individuals, I made comparisons of several traits between single-brooded and double-brooded birds in their debut breeding (Fig. 1). The only significant difference emerged in timing of breeding (i.e. fledging date). Single-brooded females bred about 15 days later than double-brooded females in their debut breeding. The fledging date of the second brood of debut-breeding double-brooded females was 37 days after their first brood (i.e. 23 June vs. 30 July). By calculation, a hypothetical second brood of the single-brooded females would have fledged around 15 August (first brood fledging date 10 July; Fig. 1). Thus, the later the breeding starts, the smaller the chances for a second clutch. A debut fledging date later than 5 July never led to a second clutch (Fig. 2).

For males, there was a similar difference in fledging date between single-brooded and double-brooded birds as for females (Fig. 1). In addition, double-brooded males had a suggestively larger first brood than single-brooded ones.

For both sexes, the first brood tended to be larger than the second brood in the debut year though not statistically significantly (females: mean 3.6 ± 1.4 (SD) vs. 3.4 ± 1.6, t = 0.15 NS; males: mean 4.3 ± 0.8 vs. 3.3 ± 1.7, t = 1.95, P < 0.1).

Ample access to good nest sites prevails in the study area. Not surprisingly, there was no difference in nest-site use between single-brooded and double-brooded birds (Fig. 1).

Table 1. Longevity of breeding Rock Pipits and the reproduction rate as measured by the number of produced broods. Percentage of double broods in parentheses.

		Females			Males		
		No. of indiv.	No. of broods		No. of indiv.	No. of broods	
Breeding life-span (years)	1	19	27	(59.3)	13	18	(38.5)
	2	5	13	(69.2)	3	9	(88.9)
	3	1	5	(80.0)	3	11	(54.5)
	4	..	..		3	18	(77.8)
	5	1	9	(88.9)	1	7	(85.7)
	6	1	11	(90.9)	..	..	
Mean		1.59	2.41		2.04	2.78	
SD		1.25	2.39		1.36	2.07	
Total		27	65		23	64	

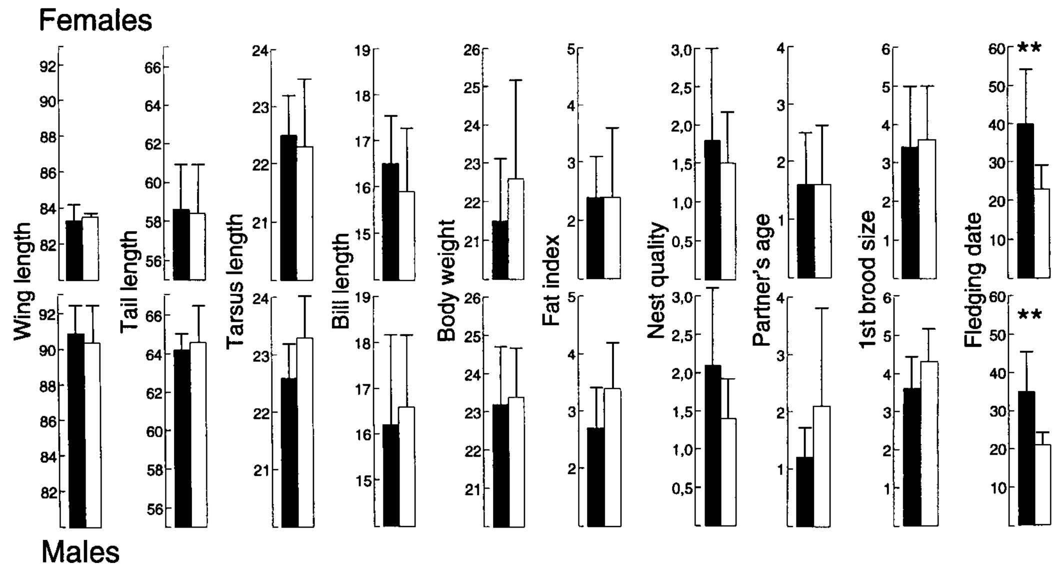

Fig. 1. Comparison of characteristics of single-brooded and double-brooded female and male Rock Pipits in their debut breeding. Mean + SD. Black columns: single-brooded (n = 15 females, 10 males), white columns: double-brooded (10 females, 10 males). t-test has been used, Mann-Whitney for nest quality and partner's age. Statistically significant difference (P < 0.01) marked with **. Rest of the differences were not significant. For fledging date, Day 1 = 1 June.

3.3. Breeding experience of the mate

There was no tendency for single-brooded birds to pair with first-year mates and double-brooded birds with older mates or vice versa (females: χ^2 = 0.132, df = 1 NS; males: χ^2 = 0.514, df = 1 NS). Thus, breeding experience of the mate did not affect whether an individual was to become double-brooded or to remain single-brooded.

4. Discussion

To reproduce once or to reproduce twice within a season seems to be associated with timing. Single-brooded birds were apparently too late to begin a second brood in their debut year, possibly due to concurrent constraints of moult and breeding. Wing moult already commences while feeding the last brood within a season (own obs.) and is well underway at the hypothetical fledging date of the second brood of single-brooded birds (15 August).

Single-brooded birds were not morphologically different from double-brooded birds, nor was there any sign of poorer physical condition in terms of body weight and fat reserves at the start of the breeding season.

No evidence of selective mating favouring experienced partners among debut breeders in any of the two groups could be detected.

I conclude that to become an early breeder (leading to double-broodedness) or a late breeder (leading to single-broodedness) is partly due to chance factors (e.g. earliness/lateness of the spring). The occurrence of double-broodedness was at its lowest during 1985–87 when there was a marked low in the entire breeding population at Söderskär (Fig. 3), presumably due to elevated mortality during the harsh winters in NW Europe (see also Herremans 1987, Larsson 1994). The remaining pairs bred abnormally late then, the median fledging date being 1 July. Another low in the proportion of double broods occurred in 1993, possibly due to the increasing proportion of recruits (75%). As a whole, the probability of producing a second clutch decreases abruptly after the end of June.

My observation of the slightly smaller second brood (compared with the first one) of the double-brooded birds in their debut is consistent with the results of Askenmo and Unger (1986) from

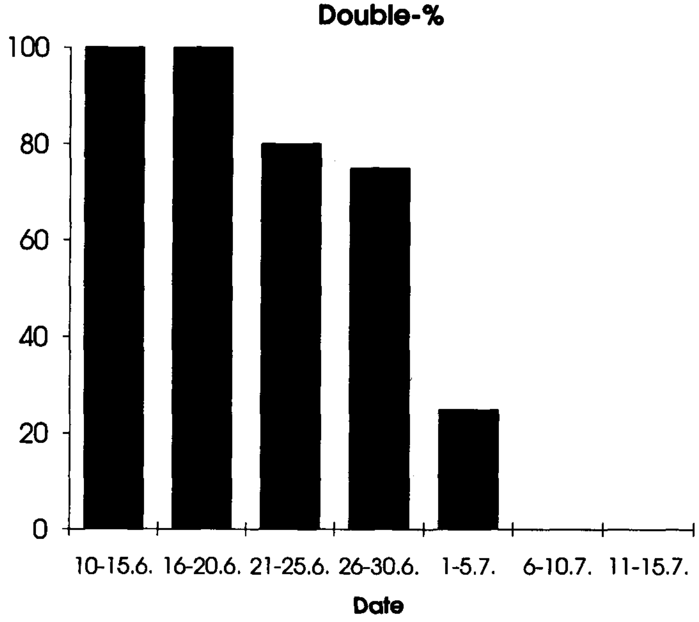

Fig. 2. Percentage occurrence of double broods in relation to timing of breeding. Date means fledging dates of the first brood (n = 27 successful broods during 1983–93).

the west coast of Sweden. In subsequent years, with increasing breeding age (up to 4 years, Askenmo & Unger 1986), the second brood becomes larger than the first one within a season. This indicates that producing a second brood in the debut year is a demanding process, probably due to a slightly delayed start of first-time breeding as a whole. Therefore, many Rock Pipit females start their breeding career prudently as single-brooded. There is no constancy in remaining single-brooded, and the occurrence of double-broodedness increases with increasing experience (age) (Table 1). Three of the four single-brooded females, which after their debut year returned to the study site, became double-brooded the next year and remained so for the rest of their lives. In addition to becoming double-brooded, they also advanced their timing of breeding by adjusting to the average timing of double-brooded birds (fledging date of the first brood shifted from 5 and 8 July to 25 and 21 June in two females, the third one failed in producing fledglings).

In yearling females, the overall heavy mortality curtailed the breeding career of single-brooded and double-brooded individuals at a roughly similar rate. For yearling males, there was a slight tendency for double-broodedness to be linked with higher survival prospects than single-broodedness. This could mean that double-brooded males are, in fact, of higher quality. Another explanation for the difference between the sexes is that first-time breeding — and breeding as a whole — really is a demanding process and that females are more heavily strained than males.

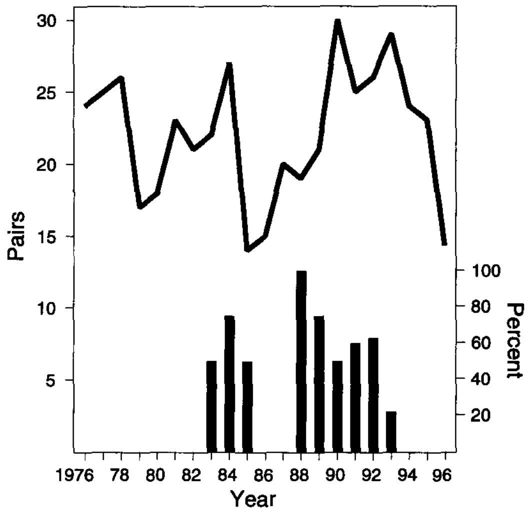

Fig. 3. Number of breeding pairs over the entire Söderskär area during 1976–96 (graph), and the percentage of double broods on the three study islands during 1983–93 (staples). There were no double broods during 1986–87. Harsh winter/late spring occurred in 1979, 1980, 1985–87, and 1996.

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Selostus: **Kerran kesässä vs. kahdesti kesässä pesivien luotokirvisten tuotannollinen elinikä**

Pienessä värirengastetussa luotokirvispopulaatiossa Söderskärillä vuosina 1983–92 luotokirvisen elinikä oli pienten varpuslintujen tapaan varsin lyhyt: naaraiden tuotannollinen elinikä oli keskimäärin 1,6 vuotta, ja ne tuottivat keskimäärin 2,4 pesyettä, koiraiden vastaavasti 2,0 vuotta ja tuotos 2,8 pesyettä (Taulukko 1). Pesiminen kerran kesässä oli yleisintä ensipesijöiden keskuudessa; myöhemmällä iällä linnut yhä varmemmin pesivät kahdesti kesässä. Talvikauden kuolevuudessa (laskettuna paluuprosentteina keväällä) ei ollut merkitsevää eroa sen suhteen, oliko yksilö pesinyt ensimmäisenä kesänään yhden kerran vai kahdesti.

Useista mitatuista muuttujista vain pesinnän ajoittuminen erosi merkitsevästi ryhmien välillä: kerran kesässä pesineet linnut aloittivat pesintänsä kaksi viikkoa myöhemmin kuin kahdesti pesineet (Kuva 1). Täydellinen sulkasato ajoittui molemmissa ryhmissä päällekkäin pesinnän loppupuolen kanssa eikä ilmeisesti mahdollistanut myöhään aloittavien parien toista pesintää. Pesiminen vain kerran kesässä oli yleisintä ankarien talvien jälkeisinä vuosina, jolloin myös kannankoko huomattavasti pieneni (Kuva 3). Ilmeisesti kevään ajoittuminen osaltaan säätelee pesinnän alkamista eli sitä, kuinka monen yksilön ylipäätään on mahdollista olla aikainen ja tuottaa kaksi pesyettä. Laatueroihin yksilöiden välillä viittaa kahdesti kesässä pesineiden koiraiden suuntaa-antavasti parempi selviytyvyys ensimmäisenä pesinnän jälkeisenä talvena; naarailla pesinnän suurempi rasitus saattaa peittää ilmiön pienessä aineistossa.

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