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Laying of replacement clutches in the Willow Warbler Phylloscopus trochilus in Lapland, Sweden

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Clutch size and the number of young, 8 d old, were determined for 23 individually ringed females of the Willow Warbler *Phylloscopus trochilus* in a study plot in the subalpine birch forest (550 m a.s.l.) at Ammarnäs (66°N), Swedish Lapland. Predation caused loss of nests and eggs for 17 of the females. Eleven of them laid a replacement clutch. Two of the latter laid a second replacement clutch after a second exposure of predation. Size of first clutches was 6.4 eggs compared with 5.2 eggs of replacement clutches. The average production of young was 1.3 in first clutches compared with 2.6 with both first and replacement clutches included. The study shows that the Willow Warbler is normally ready to replace lost clutches also at this high latitude and altitude, at least before hatching, delaying breeding up to two weeks. However, it is also shown, by argument, that the length of the breeding season does not allow two successful broods to be raised before the time of adult moult in late July and the decline of invertebrate food in August.

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Introduction

Most birds are able to produce a replacement clutch only a few days after the loss of a first clutch. The time between destruction or predation of a clutch and the laying of a replacement clutch has been measured in Scandinavia in e.g. Great Tit *Parus major,* Pied Flycatcher *Ficedula hypoleuca,* and Redwing *Turdus iliacus.* The interval was found to be 3–13 d, 5–10 d (von Haartman 1969), and 4–6 d (Arheimer 1978) in those three species, respectively.

This study shows that replacement clutches were common in the Willow Warbler *Phylloscopus trochilus* in the subalpine birch forests of the Ammarnäs region, Swedish Lapland, in 1975, a year with heavy nest predation. The total production of young in the study population was doubled by the replacement broods, which means that the effect of predation was correspondingly reduced.

Study area and methods

This study is a part of a general investigation of the Willow Warbler, conducted since 1974 in subalpine birch forests at Ammarnäs, Swedish Lapland (65°58′N, 16°17′E). It was carried out in a 20-ha plot located at 550 m a.s.l.

In 1975, we colour-ringed as many Willow Warblers as possible within the study plot. We ringed 23 of the 27 females that comprised the resident population that year. Eight of them were captured on their nests with a small net and 15 were caught in mist nests.

The density of the Willow Warbler on the slope where the study plot was situated was slightly lower than average in 1975: 133 pairs km^{-2} against a mean of 158 pairs km^{-2} in 1966–1976.

The density of small rodents was very high in 1974. This caused a good production of young and a high density of their predators, the red fox *Vulpes vulpes,* the

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stoat *Mustela erminea,* the weasel *Mustela vulgaris,* and birds of prey. Then the rodent populations crashed in the spring of 1975, after which the predators shifted to birds. Therefore, many Willow Warbler nests were preyed upon in 1975.

Results

In the study plot all the 23 individually ringed females could be coupled to their respective first nests. Seventeen of them lost their first clutch. Eleven of these seventeen females laid a replacement clutch, and two of them even a second replacement clutch after having experienced a second predation (Tab. 1). Predation occurred before hatching in twelve of the thirteen cases; in the thirteenth case the time of predation could not be determined. The time of predation was fairly evenly spread between laying and hatching. The cause of nest destruction or desertion was known to be predation in two further cases, but no replacement clutch was found.

The nest for the replacement clutch was built 20–110 m away from the earlier nest (mean = 55 m, n = 13). The number of days between predation and the laying of the first replacement egg was 4–8 d (mean 5.8 d, n = 8). Clutch size, total number of eggs per female, and the number of young at an age of 8 d are shown in Tab. 1 (normal nest time is 12 d, but checks were not made after the 8th d because the young then tend to leave the nest prematurely if disturbed.

Six of the eleven replacement clutches resulted in young at an age of 8 d. With the exception of the two second replacement clutches the further destiny of the other five nests is unknown. The average production of the 23 females was 1.3 young for the first clutch and 2.6 young with the result of the replacement clutches added.

Tab. 1. Clutch size and number of young (8 d old) in first and replacement clutches of the Willow Warbler *Phylloscopus trochilus* at Ammarnäs, Swedish Lapland. No. = Female number. 1st = 1st clutch. 1st R = 1st replacement clutch. 2nd R = 2nd replacement clutch. * = full clutch size uncertainly established. E = number of eggs. Y = number of young.

No.	1st		1st R		2nd R	
	E	Y	E	Y	E	Y
1	6	5				
2	7	5				
3	5	3				
4	5	4				
5	6	6				
6	?	7				
7	6*	0	5	4		
8	*	0	6	6		
9	7	0	5	4		
10	7	0	6	4		
11	5*	0	4	2		
12	5	0	5	5		
13	7	0	3*	0	5	5
14	6	0	3*	0	5	0
15	6	0	5	0		
16	7	0	5	0		
17	?	0	6	0		
18	4	0				
19	6	0				
20	7	0				
21	5	0				
22	5*	0				
23	6	0				
All		30		25		5
Laying date 1st egg						
Mean	17 jun		29 jun			
Range	10–30 jun		23 jun–7 jul		3 jul	
n	20		9		1	

Discussion

A replacement clutch was found for 11 of the 17 nests which were preyed upon. The other six females either did not lay again because they were physiologically not able to do so or because they had died or laid a replacement clutch that we could not find because the nest was too well concealed in the high and dense vegetation of late summer. Silverin (1980) showed that the Pied Flycatcher in Sweden is not able to produce a genuine second brood or a late repeated brood because the female refractory period starts when the nestlings are about one week old.

Seven females produced more than 11 eggs totally with a maximum of 15. This ability is no surprise since it is well known that birds have a considerable capacity to lay eggs. A Yellow-shafted Flicker *Colaptes auratus,* for example, laid 71 eggs in 72 d when the eggs were removed as they were laid (Phillips 1887). Similarly, a House Wren *Troglodytes aedon* could be induced to lay 32 eggs during one breeding season (Cole 1917).

A decline in clutch size with the progress of the season has been shown in many species (Klomp 1970). That decline is partly the result of the fact that replacement clutches are smaller than first clutches (Lack 1966). In the present Willow Warbler material the replacement clutches were significantly smaller (5.2 eggs) than the first clutches (6.4 eggs); ($n = 5$, $p < 0.02$, one-tailed t-test for correlated means).

There are few observations of replacement clutches after predation of nests with young. Klomp (1970) mentioned that such cases are known but did not refer to any particular study. In the present investigation no such case was found.

My estimate of 2.6 young as the total average production of young is somewhat uncertain. The true figure may be slightly lower because of some predation that may have occurred during the 4 d between the 8th day,

when the estimate was made, and the 12th day, when the young left the nest. On the other hand, it is probable that replacement clutches were laid in several additional cases although this could not be confirmed. Therefore, the true production of young in 1975 almost certainly was in the range of 2.5–3.0 young per female.

The several successful replacement clutches make it evident that the Willow Warbler is fully able to bring up a new brood of young about two weeks later than normal. This gives rise to the question why the Willow Warbler does not lay two clutches every year in the Lapland. It is known from England (Cramp 1955) that the Willow Warbler is able to do so. The total time from the start of nest-building to having raised a brood is about 34 d, excluding the possible time after fledging when the young are still dependent upon both the parents. If a Willow Warbler lays its first egg in early June, which is not unusual, and if everything proceeds successfully, it would be able to start a second clutch not later than mid-July. The young of a second clutch would then fledge in the middle of August.

Several factors speak against the possibility of success if the young fledge that late. The food of the Willow Warbler contains only small invertebrates, mainly insects and spiders. Early frosts in August probably reduce the amount of food and the lower temperatures in general also reduce the availability of evertebrates. The adult Willow Warblers start moulting by the end of July. Many of the birds that we have captured at this time are almost unable to fly because they lack several primaries and sometimes all the tail-feathers. To collect sufficient amounts of food for a brood of young must be difficult for a moulting bird. The adults even seem to have difficulty in finding enough food for themselves, especially for premigratory fat accumulation, since they leave the area almost immediately after having completed the moult. Results of careful censuses show that no Willow Warblers remain in the area in late August and early September.

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Also . . .

Wille, F. and Kampp, K. 1983. Food of the white-tailed eagle *Haliaeetus albicilla* in Greenland. – Holarct. Ecol. 6: 81–88.

Six nests of white-tailed eagles in the southernmost Greenland were watched during the nestling period and food items recorded photographically by remote controlled cameras. The species composition of the food was representative even for the adult eagles' diet. Fish made up a major part of 90%, various bird species and arctic fox pups the remaining 10%. The total intake of an eaglet amounted to 50 kg from hatching to fledging. The daily requirements of fledglings, some 800 g fish food, are equal to previously reported values for older birds. The rate of food consumption of eaglets is constant through most of the nestling period.

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