Abstract Several hypotheses have been raised to explain the upper limit of clutch size at four eggs in waders (suborder Charadrii), which may play an important role in the evolution of the variety of mating and parental care systems in this group. Experimental tests of the hypotheses have produced conflicting results. It was recently suggested that the combined effects of several incubation costs of a larger clutch suffice to limit its size to four eggs in this group. Here we test the incubation-limitation hypothesis in a field experiment, in redshank Tringa totanus. We created five-egg clutches by adding one egg from another nest to a just completed four-egg clutch. Four-egg control clutches were created by replacing one of the eggs by an egg from another nest. All egg removals, additions and replacements were done before incubation started. Incubation time in five-egg clutches increased by 1 day to 24.3±0.23 days, compared to 23.3±0.32 days in four-egg clutches. Egg hatchability and nest predation rates did not differ significantly between treatments. On average five-egg clutches produced one extra chick at hatching (4.5±0.26 chicks) compared to four-egg clutches (3.5±0.27 chicks). Also when several additional costs from incubating enlarged clutches are added, redshanks by laying a fifth egg would on average increase their reproductive success at hatching by an estimated 22%. The incubation-limitation hypothesis therefore is clearly rejected in this species. Possible mechanisms behind the four-egg clutch limit in waders and ways of testing the alternatives are discussed.

Keywords Alternative hypotheses · Charadrii · Incubation limitation · Life history · Reproductive tactics

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Clutch size limitation in waders: experimental test in redshank Tringa totanus

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Introduction

The evolution of clutch size has been a central problem in life history theory since Lack (1947) placed it on the ecological research agenda, and the subsequent half-century has seen great advances in the understanding of clutch size evolution (reviewed in Roff 1992; Stearns 1992). Novel insights are still emerging, however, such as the demonstration of a strong trade-off between egg numbers and composition (Nager et al. 2000), and several aspects of clutch size evolution remain poorly understood.

One persistent unsolved problem already discussed by Lack (1947) is the limitation of clutch size in waders (Scolopacidae and Charadriidae), most of which have a rather fixed clutch size of four large eggs (Maclean 1972). Many hypotheses have been raised to explain this limitation, which has also been suggested to play a role in the evolution of some of the remarkably varied mating systems of waders, ranging from lek polygyny over monogamy and double-clutching to classical polyandry (e.g. Pitelka et al. 1974; Emlen and Oring 1977; Oring 1982; Erckmann 1983; Székely and Reynolds 1995; Blomqvist et al., in press). If incubation capacity is limited to a maximum of four eggs, double-clutching or polyandry may be the only options for increasing reproduction for a female that can produce more than four eggs (e.g. Erckmann 1983; Davies 1991). Better understanding of clutch size limitation in waders is therefore of interest from both a life history and a mating system perspective.

Lack (1947) proposed that incubation capacity in waders is limited to four eggs because their large size makes incubation of more eggs difficult (also see Andersson 1978). He later abandoned this view, and several studies have concluded that in some waders clutch enlargement to five eggs does not reduce reproductive success compared to controls (reviewed by Arnold 1999). These conclusions are, however, debatable and the reasons why clutch size is usually limited to four eggs in waders are far from clear. Some authors have argued that clutch size in waders is not limited by
incubation ability (e.g. Shipley 1984; Yoge et al. 1996; Sandercock 1997). On the other hand, Arnold (1999) reviewed a number of potential costs of larger clutches that have usually not been taken into account, such as prolonged laying and incubation periods and therefore longer exposure to predators, partial clutch loss owing to increased egg breakage, and reduced hatchability because of parental inability to warm more than four eggs. Considering all these factors, Arnold (1999) concluded that these three costs of incubation in combination are sufficient to limit clutch size to four in most waders.

We test here the importance of these and other factors in a clutch enlargement experiment in redshank Tringa totanus, finding that the incubation-limitation hypothesis does not explain why redshanks only rarely exceed a clutch size of four eggs. Clutch size limitation in waders therefore remains a poorly understood life history problem, in spite of much research. We review potential limiting factors and suggest possible tests.

Materials and methods

The experiment was done at two coastal sites on the Swedish west coast in 1998: Båtafjorden (57.15N 12.08E) and Ölmevalla (57.23N 12.07E). Both are cattle-grazed coastal pastures with abundant breeding waders, mainly lapwing Vanellus vanellus and redshank. About 40 pairs of redshank breed at Ölmevalla, and over 100 pairs at Båtafjorden. In order to find nests before the clutch was full, we started searching for redshank nests well before they began laying eggs.

The nest is difficult to find at this stage, because there is usually no bird to flush from it before the clutch is full. Nests were well hidden in tufts or carpets of 1–2 dm high standing dead grass from the previous year; egg laying started when the present year’s grass was a few centimetres high. Many redshanks placed their nest 5–20 m from the more open and visible nests of lapwings (Cramp and Simmons 1983), which start earlier and by their nest defence offer some protection against nest predators, also to redshanks breeding nearby (e.g. Göransson et al. 1975). Many nests lay in grass fringing small brackish-water ponds that were scattered over the area. In order not to reveal nests to hooded crows Corvus cornix, when searching we often bent down, spent the time

Results

Estimated nest survival, number of hatching eggs per clutch, hatchability (proportion of hatched eggs per nest), incubation time and hatching asynchrony for experimental (five eggs) and control (four eggs) clutches are shown in Table 1.

Two five-egg clutches and one four-egg clutch were trampled by cattle, and one four-egg clutch was deserted because one of the parents was taken by a raptor. All these clutches were excluded from further analyses. Predation was usually all or none; partial losses only occurred in one out of 16 five-egg clutches and in none of the 11 four-egg clutches (P>0.39, χ²=0.71, n=27). The clutch with partial predation is excluded from analyses in Table 1. Egg predation was similar in four- and five-egg clutches: 8 out of 11 four-egg clutches hatched at least one egg, and so did 12 of 15 five-egg clutches (P>0.66, χ²=0.19).

Hatchability per egg was similar in four- and five-egg clutches (Table 1; P>0.79, n=20). Accordingly, five-egg

Table 1 Outcome of experimental (five-egg) and control (four-egg) clutches of redshank

<table>
<thead>
<tr>
<th>Clutch size (n)</th>
<th>Proportion with egg at least one hatching</th>
<th>No. of hatching eggs per nest</th>
<th>Hatchability b</th>
<th>Incubation time c (days)</th>
<th>Hatching asynchrony d (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 (15)</td>
<td>0.80 (12/15)</td>
<td>4.50±0.26</td>
<td>0.90±0.05</td>
<td>24.27±0.23</td>
<td>&lt;31±4.74</td>
</tr>
<tr>
<td>4 (11)</td>
<td>0.73 (8/11)</td>
<td>3.50±0.27</td>
<td>0.88±0.07</td>
<td>23.25±0.32</td>
<td>&lt;28±4.00</td>
</tr>
</tbody>
</table>

a In successful nests, i.e. those where at least one egg hatched
b Proportion of eggs hatching in nests that were not preyed upon or abandoned before normal hatching time
c Days from the fourth egg was laid until the last egg hatched
d Hours between hatching of first and last egg in the clutch