

Guarding your Mate and Losing the Egg: An Oystercatcher's Dilemma

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On the island of Schiermonnikoog, which borders the Dutch Wadden Sea, Oystercatchers *Haematopus ostralegus* have been individually colour-marked since 1983 by Jan Hulscher of the Zoological Laboratory of the State University of Groningen. Pairs defend breeding territories on the saltmarsh, where they can obtain little food, and defend feeding territories on the nearby intertidal flats. Pairs breeding on the edge of the saltmarsh defend an adjacent area of the mudflat. They will be designated as 'residents', while the pairs breeding further 'inland' will be called 'leap-frogs'.

Several different and independent lines of evidence indicate that during egg-laying the loss of eggs to predators (mainly Herring Gull *Larus argentatus* and Common Gull *Larus ca-*

Table 1. Rate (eggs per hour) at which eggs disappeared from complete and incomplete clutches.

laying: 1st egg	0.0129
laying: 2nd-3rd egg	0.0010
clutch complete	0.0001

nus) is much higher than when the clutch is completed. Table 1 presents the rate at which eggs disappeared from nests that were visited twice a day. It appears that the difference in predation rates is due to imperfect nest defence on the part of the parents (Figure 1). In this case we measured 'nest defence' as the total amount of time during which at least one parent was present on the saltmarsh. When the clutch is complete it hardly ever happens that no parents are present and aggressive Oystercatchers have few problems in chasing away gulls.

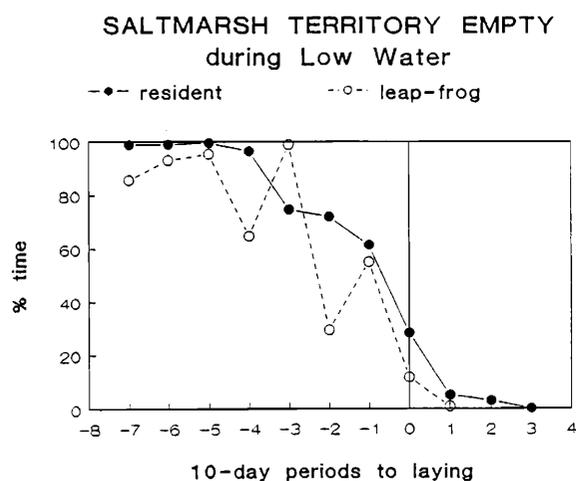


Figure 1. Percentage of time during low water when the saltmarsh territory was empty relative to the moment of egg-laying for resident and leap-frog pairs. Resident pairs are nearer to the nest when feeding in their mudflat-territory.

What prevents parents from attending their nests properly during egg-laying? Before egg-laying, the pair moves as a unit, switching back and forth between the saltmarsh and the mudflats. Figure 2 shows that this association behaviour starts two months before egg-laying and is abandoned during incubation. However, during egg-laying the birds still associate more often than expected by chance (expected time together in the same area calculated from the time each pair member was observed in those areas).

One possible explanation for this association behaviour is that it is 'mate-guarding' by the male to make sure that his female does not engage

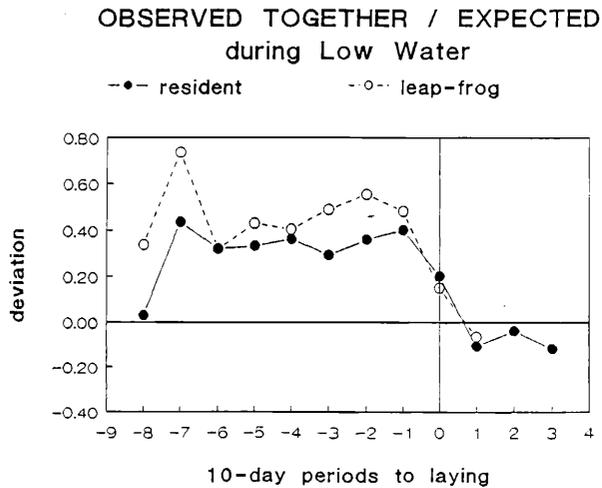


Figure 2. Deviation from the value 1 of the ratio of time observed in the same area divided by the time expected to be together if the birds distributed their activity independently from one another, relative to egg-laying for resident and leap-frog pairs. A positive score indicates that the members of the pair were more often together than expected by chance.

in Extra-Pair Copulations (EPCs). Males and females take more or less equal shares in parental duties and the chicks have to be fed until well after fledging, so the cost of cuckoldry must be high for the male. Figure 3 shows that copulation rates are high and that copulation continues during egg-laying, suggesting that fertilization is possible at this stage. Indeed, results from DNA-fingerprinting of 20 chicks (a cooperative project with Terry Burke from the University of Leicester) indicated an extra-fa-

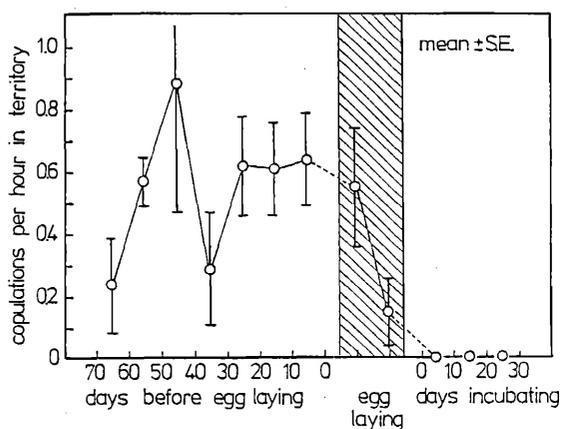


Figure 3. Copulations per hour when the pair was together in the feeding territory or the breeding territory, relative to egg-laying.

EXTRA-PAIR COPULATIONS

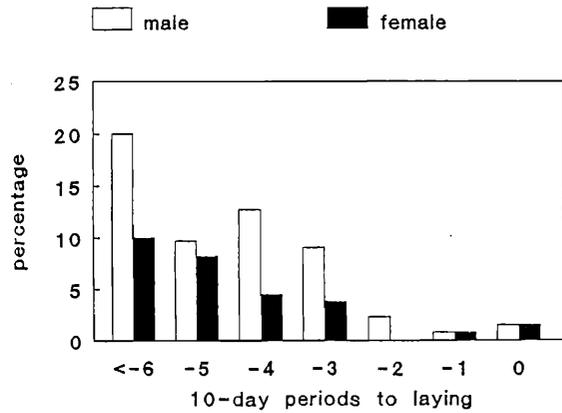


Figure 4. Percentage of all copulations with a partner other than the breeding partner for males and females relative to the moment of laying of their own clutch. We employ a very loose definition of extra-pair copulation as it does not exclude pair formation and mate changes early in the season.

ther young in the clutch of a female that was seen to copulate with another male than her own mate during egg-laying.

However, mate-guarding assumes that males follow a mixed reproductive strategy: 'Share parental duties with the female you are paired with and at the same time try to obtain sneaky copulations with other females'. We have very little evidence that males actively seek such sneaky copulations: they may even chase away strange females that invite copulation. Figure 4 shows that most EPCs occur early in the season and may represent attempts to change mate by both partners (according to the strict definitions of Westneat *et al.* 1990 (*Current Ornithology*, Plenum Press) many of these copulations would not count as real EPCs).

Alternative hypotheses which could account for the association behaviour are (1) giving up communal defence of the territory leads to an increased probability of losing the territory, or (2) the mates 'guard each other', to make sure that no alternative pair bonds are formed. The two hypotheses are not mutually exclusive as several instances of territory usurpation by single individuals which pair with the remaining mate, have been observed.