Search, settle, reside & resing

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In many territorial species, such as the oystercatcher, a fraction of all mature individuals does not breed. These mature nonbreeders, or floaters, often behave inconspicuously and little is known about how they organise their lives and attempt to settle in the population. The acquisition of a territory by a floating oystercatcher is usually preceded by becoming familiar with a small area, mainly through short inspection visits (intrusions) to occupied territories. We observed intrusion behaviour of floaters (chapter 2), subsequently removed breeding birds and then observed floaters as they were filling these artificially created vacancies (chapter 3). Across years floaters returned to the same locations and those that became familiar with the area and its inhabitants filled 80% of the experimentally created vacancies (chapter 3). The settlers were sometimes neighbours or floaters with a former breeding history nearby, but were usually floaters with an intrusion record nearby. These results suggest that local information is essential for territory acquisition. Vacancies that were not occupied by intruding floaters tended to be located in areas where less intruding floaters were active prior to removal.

In chapter 4 local recruitment is further analysed. Assumptions and predictions of a settlement model developed for this species (Ens *et al.* 1995) that proposes that birds in high- and low quality sites are phenotypes with an equal fitness pay-off, were tested. The main prediction of this model, that settlement in a high quality territory is counter-balanced by a later onset of breeding, was not supported by our field observations. Another implicit assumption of this model, in which fledglings were used as fitness currencies, was that all fledglings produced are identical in phenotypic quality. However, in the field we observed that only birds born in high-quality territories managed to settle in high-quality territories, while birds settling in low quality territories originated from both territory types. Apparently conditions experienced during early development have long lasting effects, and only those raised with a 'silver spoon' can look forward to a bright and shiny future. In contrast to expectation, local recruits born in low quality territories were larger at fledging and tended to be heavier compared to recruits born in high quality sites, suggesting that the disadvantage of being raised in a poor quality territory can only be overcome by individuals that grew very well. Local recruits were mostly males (indicating female biased dispersal) and local dispersal distances were larger for females than for males. Females that settled farther from their natal site were heavier and larger at fledging compared to those settling nearby, but this relation was absent for males. The probability to produce a recruit varied significantly with territory quality: Only 9% of all fledglings from low-quality territories managed to recruit, while 23% of all fledglings from high quality territories did. The effect of natal territory quality on recruitment rate and settlement place disagrees with key assumptions of the settlement model. We conclude that it is unlikely that birds in high- and low quality territories have similar expectations concerning lifetime reproductive success, and therefore focus in chapter 5 on an alternative hypothesis suggesting that birds in high quality

territories are of superior phenotypic quality. We investigated social dominance in the field, and in captivity, in relation to the quality of the breeding territory. In the field, birds with high quality territories won fights more often compared to those occupying low quality territories, but this difference was not apparent in a small data-set of captive birds.

In chapter 6 we investigated the fitness consequences of divorce. Two divorce-types can be recognised: in *desertions* the disruption of the pair bond is initiated by one of the pair members, and in *usurpations* by a conspecific outside the pair. Divorce participants differed strongly in their fitness prospects, depending on the type of divorce, the role played in the divorce and the quality of the territory where the divorce took place. Changes in social status (*i.e.* without a breeding territory or occupying a high- or low quality territory) in relation to divorce showed that birds *taking the initiative* to leave their partner increased in fitness, relative to birds that were *forced* to leave their partner. Individuals who remained in their territory after divorce did not loose their territory if their partner was expelled, but lost it (or obtained a territory of lower quality) if their partner deserted. Survival after divorce was significantly lower for birds that were expelled than for those deserting. Divorce rate, and especially desertion rate, was higher among occupants of low- than high quality territories. In high quality territories usurpations increased with increasing breeder mortality in the population, but in low quality territories this relation was absent. Divorce may lead to a former breeding bird skipping breeding for at least one breeding season, later followed by a prolonged breeding career. This so-called intermittent breeding (chapter 7) can be the result of an active choice by the focal individual, adaptively skipping a breeding attempt (residual reproductive value hypothesis). In contrast, an individual can also be forced by conspecifics to leave its breeding site and partner and refrain from breeding due to saturation of the breeding habitat (competition hypothesis). The main cause for intermittent breeding in high quality sites was death of a mate, while in low quality sites divorce was the main cause. Evidence in favour of the competition hypothesis was abundant, in 93% of the cases birds were forced to cease breeding due to pressure from conspecifics. There was no association between intermittent breeding and promotion to a territory of better quality. Instead oystercatchers returned to breeding habitat of similar quality and at a very close distance (median distance 128m) from the previous location. Intermittent breeding lasted on average 2.4 years, with a maximum of nine years and the duration varied with the quality of the territory obtained after the pause, but in contrast to expectation birds who continued breeding in a high quality territory acquired this on average faster than those in a low quality territory, indicating that birds in high quality sites are better competitors.

In chapter 8 we analyse national and local trends for the oystercatcher and connect these findings with our behavioural observations. Over the past twenty years wintering numbers in the Dutch Wadden Sea are decreasing by 2% per year

and breeding numbers on mainland meadows are decreasing by 5%. During the same period breeders on study plots on Texel and Schiermonnikoog decreased by 8.7% and 4.5% per year respectively. On Schiermonnikoog decline in numbers was most profound in low quality territories (-7% and -13% per year in two sub-areas) and much less extreme in high quality territories (-1.1% and -1.9%). Adult survival was not affected over the years, but the birds laid later at both sides and fledgling production decreased over time. Fledgling production decreased with 0.05 young/pair/year in high quality territories and with 0.02 young/pair/year in low quality territories. Fledgling production was correlated between Texel and Schiermonnikoog and the decrease in number of breeders and the increase in laying date were identical at these two coastal sites, located on opposite extremes of the Dutch Wadden Sea. This suggests that the observed changes are caused by processes operating over a large scale. From previous work we know that oystercatchers have to invest many years at the same location in order to obtain a territory. This strong site fidelity limits the options of 'waiting' nonbreeders and explains why breeding numbers can decline despite the presence of unsettled breeders. New findings suggest that oystercatchers in winter are also site-faithful and in combination with a decline of food stocks, this may explain why oystercatcher numbers have decreased over the last decade.