Site fidelity in Oystercatchers: An ecological trap?

Jeroen Onrust

Bachelor Thesis Animal Ecology
Supervisor: Prof. Dr. Theunis Piersma
Second reader: Prof. Dr. Joost M. Tinbergen
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Table of Contents

ABSTRACT **2**

INTRODUCTION **3**

ECOLOGICAL TRAPS 3

SITE FIDELITY **4**

WHY SITE FIDELITY? 4
BEING FAITHFUL TO YOUR MATE 5

THE DEDICATED OYSTERCATCHER **7**

THE OYSTERCATCHER SOCIETY 7
ACQUIRING A TERRITORY 8
THE SPECIALIST 11

HABITAT CHANGE **12**

CAUSES OF POPULATION DECLINE 12
HABITAT LOSS 14
CLIMATE CHANGE 14

DISCUSSION **16**

IMPRISONED ON THE SALT MARSH 16
LOOKING TO THE FUTURE 18

REFERENCES **19**

SUMMARY **22**

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Abstract

The population of Oystercatchers (*Heamatopus ostralegus*) in the Netherlands declined dramatically during the last two decades as a result of deteriorating food conditions in the Dutch Wadden Sea. Oystercatchers are highly territorial and show strong site fidelity which is the tendency to return to a previously occupied location. Site fidelity may be favoured because long-term familiarity with a territory and its surroundings should lead to increased individual survival and higher fitness. To acquire a territory an Oystercatchers have to build up local dominance which forces a bird to stay at one place for many years. Consequently, this site fidelity works as an ecological trap. An ecological trap occurs when a bird chooses to stay in low quality habitat although high quality territories are available. Oystercatchers decide to stay because leaving would be detrimental as they have to build up local dominance all over again. Only if food conditions and thus habitat quality will improve, the Oystercatcher population can be saved from further decline.

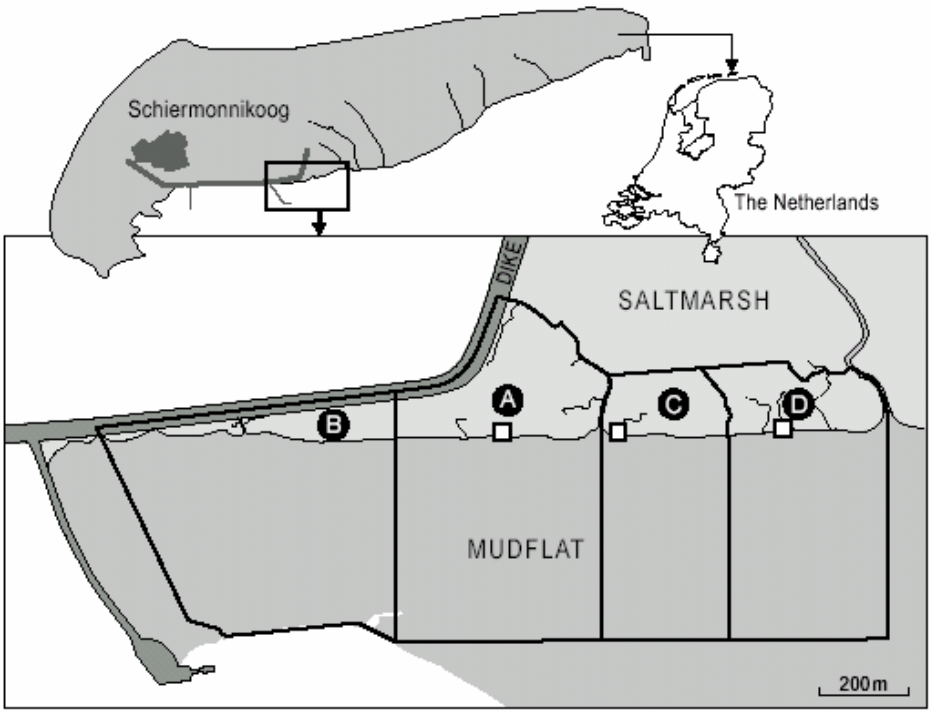
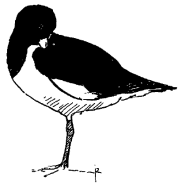


Figure 1: Study area of the Eurasian Oystercatcher (*Haematopus ostralegus*) population on the island of Schiermonnikoog in the Dutch Wadden Sea. After Ens 1992.

Introduction



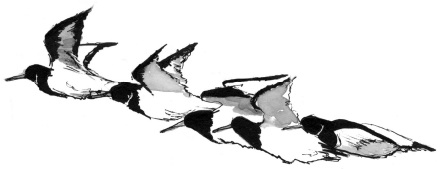
Black, white and conspicuous. With only a few words one of the most remarkable birds can be described and recognized: the Oystercatcher. The Eurasian Oystercatcher (*Haematopus ostralegus*) is a long-lived wader species inhabiting coastal and several large inland areas from Western Europe to Asia (Van de Kam *et al.* 2004).The species is mostly monogamous and highly territorial. Oystercatchers are non-migratory species, and will only migrate during severe winters. On the island of Schiermonnikoog in the Dutch Wadden Sea lives an interesting population of Oystercatchers (fig. 1). A part of this population is intensively studied already since 1983 until present and this work resulted in no less than five dissertations. The long-term population study revealed an interesting social system with birds living in low and high quality territories. Each breeding bird in the study area was individually marked with colour rings and this showed that Oystercatchers do have strong tendency to return to a previously occupied location during and outside the breeding season. This tendency is termed as site fidelity or site faithfulness (Switzer 1993).

Ecological traps

The Oystercatcher population in the Netherlands are facing a hard time. The population declined dramatically with 50% in the past twenty years (Oosterbeek *et al.* 2006). The main cause of this decline is the decreased food availability in the Wadden Sea caused by intensive shellfish fisheries (Verhulst *et al.* 2004). Despite the deteriorating habitat, Oystercatchers stayed faithful to their sites. When an individual chooses a poor-quality habitat above better alternatives, then an ecological trap can occur. An ecological trap is when an environment has been altered suddenly by human activities and in which an organism makes a maladaptive habitat choice based on formerly reliable environmental cues, despite the availability of higher quality habitat (Schlaepfer *et al*. 2002). An example of an ecological trap are Lapwings (*Vanellus vanellus*) that select lush green fields, but in intensive farming landscapes these are often highly fertilized cereal fields, and the birds usually abandon their nests as the cereals grow rapidly (Kokko & Sutherland 2001). Cooper's Hawk (*Accipiter cooperii*) occur at much higher densities in some cities than in rural areas although nestling mortality is much higher in cities because of diseases (Battin 2004). An animal is ecologically trapped when it makes a habitat choice that is based on outdated cues, resulting in lower reproductive success. So if the Oystercatchers did not move to better areas in response to the deteriorating habitat, than it seems that the site fidelity of Oystercatchers works as an ecological trap.

In this thesis I will try to give an answer on the question if site fidelity in Oystercatchers is working as an ecological trap. I will discuss the factors that determine site fidelity and why birds are site faithful with special interest in Oystercatchers.

Site fidelity



"As free as a bird" is an often used phrase to refer to the unlimited freedom a bird has. Birds can fly all over the world and explore sites to forage, to nest or to find a mate. For them, the immense world seems to be not that big at all. However, for the greater part of the birds, that world is in fact even smaller. Nowadays, it is well known that certain species only occur in certain parts of the world. No single species of bird can be found everywhere, each species typically occurs within a limited range, and often only in specific habitat or at specific times of year. During the year cycle of a bird, most birds show a tendency to return each season to a defined area or patch of breeding habitat (Hoover 2003).

Instead of being truly faithful to a certain site, many birds are actually 'as free as a bird' and are mobile to migrate to other parts of their world to benefit from optimal conditions (Gill 2007). However, even during migration individuals prefer the same staging, e.g. Greylag Geese (*Anser anser*) (Kruckenberg & Borbach-Jaene 2004) or wintering site within and between years, e.g. Red Knots (*Calidris canutus canutus) (*Leyrer *et al.* 2006). In their non-breeding grounds, birds can defend those sites with a great deal of verve. We probably all know the aggressive Robin (*Erithacus rubecula)* in backyards during winter, but also Grey Plovers (*Pluvialis squatarola*) defend a non-breeding territory on the mudflats (Turpie 1995).

Why site fidelity?

Why do birds return to the same site every year? As site fidelity is widespread, not only in birds, but also in more animal taxa (Switzer 1997), the answers lies probably in an evolutionary context. Natural selection will favour individuals that use the habitats in which most eggs hatches (precocial species) or young fledges (altricial species) successfully (Krebs 2001). A habitat is a distinctive set of physical environmental factors that a species uses for its survival and reproduction (Jones 2001). Habitats are not equal and heterogeneity between habitats results in high or low quality habitats. Habitats may differ in the abundance of food resources, vegetation structure, quality of nesting sites or the level of inter- or intraspecific competition (Schmidt 2001). Individuals that choose poorer habitats will not be that successful and consequently will be selected against. This does not mean, however, that populations in low quality habitats will not be viable. In fact they can work as 'sink' population of an outflow of individuals from the preferred habitats (Krebs 2001). These sink populations have consequently a lower fitness[1] because of lower quality of the habitat they life in. To gain the highest fitness however, it would be necessary for birds to recognize preferable habitats and thus to be able to select for it. Habitat selection refers to the process of behavioural responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Jones 2001).

When a bird finally has chosen a suitable habitat for nesting or foraging, they defend it to intruders. This territorial behaviour is common in most bird species, though the way a bird defends it territory differs. Oystercatchers for example, as I will discuss further, are territorial

[1] Fitness is a measure of the contribution of an individual to future generations (Krebs 2001).

and conspicuous while others such as most passerine birds only sing to mark their territory (Gill 2007). Besides a breeding territory, birds can maintain a feeding territory, which is especially common in seabirds (Irons 1998) and waders like Oystercatchers (Ens 1992) as their food may be some distance offshore. The selection for a preferable habitat does not really gives a confiding answer on why birds are site faithful. Preferred habitats are for the majority of species abundant, however individual birds still return to the same sites. So staying at one site or always returning to a specific site is probably for some birds more convenient than just wandering around the globe. If so, site fidelity should be beneficial. What are those benefits of site fidelity? And which factors determines how strong a bird is bonded to a certain area?

The first and important benefit is knowledge about the area. When nesting or foraging every year in the same area, individuals will become familiar with that specific area. This can be highly advantageous, as it is likely that the acquired information about the area through the years will give you a selective advantage to individuals that are not familiar with that area. A higher survival and breeding success could be achieved by knowing the best locations to forage, to hide for predators or to nest (Greenwood 1980). Besides knowing good locations, it is beneficial to have a better knowledge of potential mates and of neighbours and their hierarchical status that decreases the number of conflicts (Bried & Jouventin 2001). When staying in your territory, you are even able to maintain your social status, as I will discus later (Heg 1999).

Being faithful to your mate

Birds that show high site fidelity do often show high mate fidelity too. Monogamy refers to a prolonged and essentially exclusive pair bond with a single member of the opposite sex for purposes of raising young (Black 1996). Monogamy is common in birds and over 90 percent of all birds are considered monogamous, though strict monogamy may be the exception rather than the rule among birds (Gill 2007). For pairs that are migratory and are faithful to their mate, but will not spend the non-breeding period together, being site faithful can reunite the pairs. In this case, site fidelity functions as a meeting point. Consequently, when pairs use a specific site just to reunite, is site fidelity not just a result of mate fidelity? Cézilly *et al.* (2000) showed that in the order of Ciconiiforms[2] species that have a low divorce rate, and thus have high mate fidelity, do have a high site fidelity rate too (fig. 2). Of course, there is, as you can see in the graph, a lot of variation and there are some exceptions like some albatrosses, which show high mate fidelity despite of low nest fidelity (Bried & Jouventin 2001). Cézilly *et al*. (2000) suggest that this variation has to do with mate retention. Species with low site fidelity show more extreme differences in vocalization between individuals which make it easier to recognize mates and thus a site that functions as a meeting point is not necessary. However, for many bird species it is believed that they choose for a breeding site and not for a mate (e.g. Leach's Storm Petrels (*Oceanodroma leucorhoa*) divorced after the nest burrow was blocked, female Blackbirds (*Turdus merula*) also divorce and leave low quality sites in search for better territories; Black 1996). It could also be age-dependent, young female Tree Swallows (*Tachycineta bicolor*) have a higher tendency to change partners between years because they have a lower site fidelity (Llambias *et al*. 2008). Therefore, for some species it seems to be true that mate fidelity is a by-product of site fidelity, but it is certainly not universal among bird species.

[2] The order Ciconiiforms contains 29 families of long-legged wading birds, including storks, herons, ibises, spoonbills and flamingos (Gill 2007).

Besides monogamy, the bonding a bird has with a specific site will also be strengthening by the breeding success of the previous year. When the breeding success was high (many fledglings produced), than a bird is more likely to return in the next year to its previous breeding location. A failed breeding attempt will often lead to a new nesting site in the next breeding season (Schmidt & Whelan 2010). This is called the 'win-stay/lose-switch' rule (Schmidt 2001). This can happens also with mates. Cory's Shearwaters (*Calonectris diomedea*) tended to change, beside their nesting-sites, also their mates after a failed breeding attempt (Thibault 1994). Therefore, nest-site fidelity is also determined by age and experience, as younger individuals are less successful than adults are (Pyle *et al.* 2001).

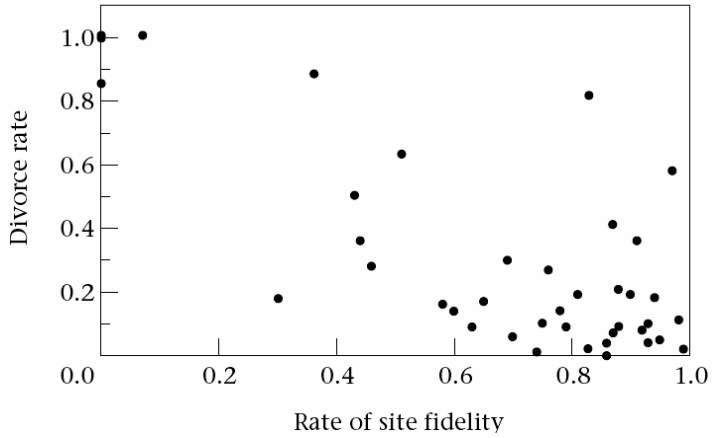
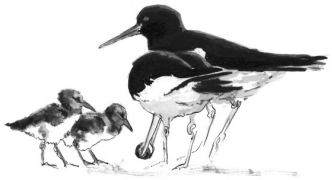


Figure 2: Relationship between divorce rate and site fidelity rate in Ciconiiforms. Divorce rate was calculated as the number of pairs where at least one partner re-paired and bred with a different partner the following year, while the previous mate was still alive and present in the population, divided by the total number of pairs where both partners were still alive and present in the population. Site fidelity rate was calculated as the number of individuals nesting within 10 m of their previous site divided by the total number of individuals in the study area over two consecutive breeding seasons. After Cézilly *et al.* (2000).

In conclusion, there are many factors determining site fidelity in birds. Site fidelity seems to be an adaptive strategy, resulting in higher breeding success and thus fitness. However, as like everything in birds, there are still many species showing different strategies. Being site faithful is thus not that beneficial as it looks like, otherwise it would be more common among birds. There should be some costs of site fidelity. When a bird has found a suitable site, there are always individuals trying to nest or forage in that suitable site as well. As a bird, you thus have to compete for a site and finally defend it. Maintaining a territory (which is in this case, the suitable site) is costly, as you have to spend time and energy to chase away intruders (Krebs 2001). The costs of competition may range from egg or chick losses resulting from disturbance by intruders, or until death if fights occur. However, birds can also choose to stay in a habitat that has become of poorer quality because of deterioration resulting in a lower breeding success too. All these costs fit perfectly for the Oystercatchers of Schiermonnikoog. As already mentioned, they defend with great effort a territory and they are an exception on the 'win-stay/lose-switch' rule as they hardly change of breeding site, even after an unsuccessful breeding season. Moreover, they are staying almost year-round in a deteriorating habitat. Time to get more in detail of this remarkable, but very interesting, bird.

The dedicated Oystercatcher



When an Oystercatchers hatches, it will be cared and protected with great effort against predators and other dangers by its parents. Juveniles hatches with eyes open and are covered with down, and are thus capable of leaving the nest soon after hatching. However, Oystercatchers are semi-precocial and the chicks will be fed for many weeks by their parents (Van de Kam *et al.* 2004). In spite of the intensive parental care, the future of young Oystercatchers is far from certain. To become as successful as their parents, they have to walk a long path before raising offspring by themselves.

The Oystercatcher society

On the Frisian island of Schiermonnikoog, Oystercatchers are studied since 1983 until present day. This study revealed an interesting social system. Oystercatchers have a great preference to nest on the edge of the salt marsh (which is on Schiermonnikoog very sharp due to erosion) with an adjacent feeding territory on the mudflats. This is because Oystercatchers do not collect food in their nesting territories on the salt marsh, but only on the intertidal mudflats. Consequently, they defend both a nesting territory on the salt marsh and a feeding territory on the mudflats. Birds nesting on the edge of the salt marsh however do not have to defend two territories as they can simply defend one large territory including a nesting and a feeding territory (Ens 1992).

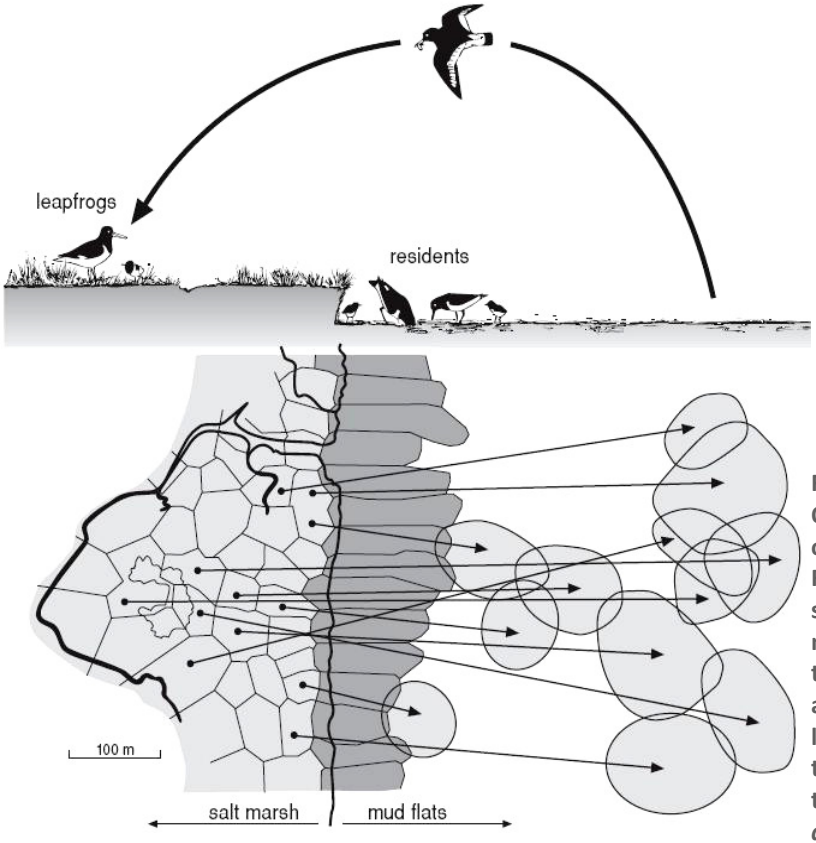


Figure 3: Map of the Oystercatcher study area on Schiermonnikoog. Resident territories are shaded dark and the nesting and feeding territories of leapfrogs are shaded light and linked with an arrow to the feeding territories on the mudflat. After Ens *et al.* (2003).

Another advantage for these birds is that they can take their chicks to the feeding grounds and feed the chicks as much food as they can find. These attractive habitats are scarce, and thus Oystercatchers compete to occupy a territory at those places. As there are more oystercatchers than high quality territories, some Oystercatchers content themselves by breeding further ashore on the salt marsh. When these birds have chicks however, they have to commute between the feeding grounds en the nesting grounds to feed their chicks. By doing so, they have to fly over the high quality territories and thus they are called "leapfrogs". Birds nesting in high quality territories are called "residents" as they do not have to leave their territory (fig. 3) (Ens 1992).

As a consequence of this social system, residents produce in some years on average three times more fledglings than leapfrogs do (Ens *et al.* 1992). This is not because of a large difference in clutch size or hatching success, but is mainly caused by the fact that leapfrog pairs do not do their utmost to provide their offspring with enough food (Van de Kam *et al.* 2004). Leapfrog parents must fly food in to their chicks and flying is energetically expensive. Leapfrog parents are constrained by the high energy costs of flying. However, when increasing its workload a leapfrog bird is able to raise more chicks and can become as successful as a resident bird (Kersten 1996). Leapfrogs seems to be lazy and do not choose for the latter option. This sounds strange because no offspring results in a low individual fitness. So why are leapfrogs putting no extra effort into their chicks and increase their fitness? When they will do so, an energetically expensive breeding season could reduce the future survival of the parents. As Oystercatchers are long-lived species, the cost to die and reproduce never again is higher than the benefit of raising a chick every year in its life (Kersten 1997; Van de Kam *et al.* 2004). After a young leapfrog Oystercatcher hatch, their parents will protect it against all dangers and they are provided with food from the mudflats. But as soon they grow up and require larger amounts of food, their parents refuse to bring more food and the chicks die of starvation. An experiment with providing the chicks with supplementary food, resulted in better growth and finally fledging, suggesting that most chicks die because of food shortage rather than low individual quality (Ens 1992). However, starving chicks are more vulnerable to diseases and when they become desperate and start wandering around begging for food, the risk of predation increases too.

Acquiring a territory

So being a leapfrog is far from ideal. Nevertheless, leapfrogs are at least able to try to raise some offspring, as a large group of all mature oystercatchers does not breed at all. These non-breeders often behave inconspicuously, but meanwhile they are gathering information about the status of breeding birds to take over their territory eventually. For a non-breeding oystercatcher, it would be better of course to acquire a resident territory because the reproductive success there is so much greater than in leapfrog territories (Ens *et al.* 1992). Acquiring a high quality territory however can take a large part of an Oystercatcher life. At the age of two or three year, young oystercatchers leave their wintering grounds and return to the breeding grounds (often were they grew up) to join the club of non-breeders (Bruinzeel 2004). The earliest possible age of breeding is probably three in females and four in males, but acquiring a territory and finally starting with breeding can take several more years (Ens *et al.* 1996). Every year a mature bird does not breed is a wasteful year as it misses an opportunity to reproduce. Many birds (especially larger birds) wait at least two years after hatching before they start breeding. This is advantageous because a young and inexperienced bird has a higher chance to die in its first breeding season, resulting in a low fitness (Van de Kam *et al.* 2004). A

bird was successful in its life when it successfully raised at least two offspring to replace itself and its mate to maintain the population (Gill 2007) and for a long-lived species such as the Oystercatcher, it is not that disastrous to be unsuccessful in a certain year.

Non-breeding Oystercatchers (including never bred young and former breeders that have lost their territory) have to make decisions; do they compete and wait a long time to obtain a high quality territory (with the risk of being injured or even killed before that) or do they acquire a less risky and with a short wait, but low quality territory? As low quality territories are more abundant on Schiermonnikoog, Oystercatchers have more opportunities to obtain a leapfrog territory. Nonetheless, a large group of non-breeders chooses to wait until a resident territory becomes available (Heg 1999). Actually, instead of waiting passively they pick out an alluring resident territory and visit it many times for many years until they finally obtained it or until they die (Bruinzeel 2004). During those visits, they try to evict the breeders by intrusions and hovering ceremonies above the nesting territories (Heg *et al.* 2000). Therefore, even these birds are faithful to their 'intended' territory and their strategy too. When a young Oystercatcher have decided to wait for a long (resident) or short (leapfrog) time, they do not change their decision (Ens 1992). On their long way to acquire a resident territory, non-breeding oystercatchers often defend a feeding territory on the mudflats nearby the resident territory. By doing so, they are building up local dominance, which is of great importance by finally taking over a breeding territory (Heg *et al*. 2000). Local dominance is site-dependent, which means that an Oystercatcher only wins a fight when in its own territory (Ens *et al.* 1996). This behaviour is also common in other territorial birds, such as males Steller's jays (*Cyanocitta stelleri*), for which the ability to win a fight decreases when the distance from nesting site increases (Gill 2007). This demonstrates one of the benefits of being site faithful; owners of a territory can use familiar details of its territory to its own advantage. Therefore, when an Oystercatcher has a territory close to the desired territory, it has a greater chance to eventually take over. This can happen with leapfrogs too, that share their border with a territory they are managing to move into eventually. So being site-faithful is also of great importance when a non-breeding Oystercatchers is attempting to obtain a breeding territory. The decision those Oystercatchers make also depends on site fidelity, or with other words, it depends on how an Oystercatcher develops a bonding with a territory on the edge of the salt marsh or further ashore. Young birds do often have a tendency to return to their breeding grounds[3]. Bruinzeel (2004) showed that for Oystercatchers, the offspring of residents had a higher probability to settle in a resident territory than leapfrog offspring had even when young Oystercatchers were of equal conditions at fledging. This could be because resident offspring are more familiar with the area and their inhabitants.

After many years (average age is seven, Bruinzeel 2004) and after a great devotion, a non-breeder can acquire a territory and can finally start producing offspring .There are several ways a non-breeder can take over a territory. The most common strategy is to build up local dominance and squeeze between breeding territories (Heg *et al.* 2000). This strategy is more successful when working as a pair, like leapfrog neighbours often try. Non-breeding oystercatchers could also already have formed a pair bond with another before they have acquired a breeding territory (Bruinzeel 2004). In this process, it is thus important that an oystercatcher is faithful to its mate, or not. In the monogamous oystercatcher divorces often occur because of territory battles. There are several paths to divorce for an oystercatcher; one partner may desert the other, one partner may be chased away by a usurper and an old partner

[3] The tendency to stay near one's birthplace is also called 'natal philopatry' (Krebs 2001).

may find itself pre-empted by a new bird that arrived earlier (Ens *et al.* 1996). These are all opportunities for a non-breeding to take over a territory and as they are always probing the status of the breeding birds, they know exactly when it is the right time to do so. I will not discuss the consequences and the reasons of a divorce for a breeding bird, but you can imagine that a breeding bird is better of when it can stay in its own territory or moves to another of the same or even higher quality.

In conclusion, there are many strategies to acquire a high quality territory and an Oystercatcher have to make important decisions. These decisions can only be applied to a certain area. It does not work for an oystercatcher when it leaves the area after many years to try to acquire a territory somewhere else. They have to build up local dominance all over again in the new area. Although, oystercatchers are birds and are thus free to move all over the world, they are actually caged in their local and social system.

Is this notable system on the salt marsh of Schiermonnikoog unique? Though it is one of the best-studied populations in the world, studies at many different sites have found that Oystercatchers that can take their chicks to the feeding grounds are more successful than Oystercatchers that have to bring food to their chicks (Van de Kam et al. 2004). The Eurasian Oystercatcher population on the island of Skokholm (Wales, UK) shows a similar society as on Schiermonnikoog. Birds foraging on terrestrial arthropods and earthworms are like residents and do not have to bring food to their chicks. As a result, they are more successful than birds foraging on marine food, which have to fly back and forth between the feeding and nesting territories to provide their chicks with food, just like the leapfrogs on Schiermonnikoog (Safriel 1985).

Besides Oystercatchers, in many other bird species there are groups of individuals breeding in low quality habitats especially when high qualities are scarce. The condition to obtain a high quality territory depends mostly on a birds' social status, and the older and the more experienced a birds is, the more likely it will breed in a high quality territory (Krebs 2001). This social status is for many species also of great importance to become a breeding bird. In Long-tailed Manakins (*Chiroxiphia linearis*) for example, two males cooperate for some years to give a peculiar synchronous show to females in which one of the males jump over the other and performs a hovering "buterfly" flight. One of the males has an higher social status than the other and when the females is impressed by the show, only the male with the highest social status will mate with her (Heinrich 2010). This seems to be disadvantageous for the low status male, but as soon the high status male has died, he can take over his position and find another low status male to perform new shows and finding a mate to copulate.

Another remarkable feature of Oystercatchers is the long time they have to invest to become a breeding bird, in other species it can take quite some years too. To come back on the Manakins example, it takes a male four years to acquire their adult plumage so they can start with their shows and from then they have to acquire higher social status to final become a breeding bird (Heinrich 2010). In bird species, but also in other taxa, where the female chooses a male, males have to compete on display grounds, also called 'leks'. The most dominant males however, will mate most frequently (Gill 2007). Males with a low social status can only become successful when its dominance increases which is a matter of age, experience and ability. The time it takes to become a breeding bird, or to reproduce, depends in many species, including the Oystercatcher, on social status. Climbing the social ladder will cost effort, but most of all lots of time.

The specialist

As already mentioned, Oystercatchers are semi-precocial and chicks are fed by their parents for several weeks. This is quite unusual amongst waders. In most precocial species, chicks forage by themselves and the parents lead them to feeding grounds (Gill 2007). This kind of parental care is common in close related species such as the Avocet (*Recurvirostra avosetta*), Lapwing (*Vanellus vanellus*) and Common Redshank (*Tringa totanus*) (Van de Kam *et al.* 2004). Nonetheless, the Oystercatcher' parental care have more in common with that of gulls and other seabirds from which the chicks are also precocial and are fed by adults (Schreiber & Burger 2001) but they are in contrast with Oystercatchers sedentary. We thus might say that Oystercatchers' parental care is quite exceptional. This unique behaviour might be caused by their food preferences. Oystercatchers foraging on mudflats mainly prey on bivalves such as Mussels (*Mytilus edulis*) and Cockles (*Cerastoderma edule),* though worms and crabs can occur in their diet (Hulscher 1996). Opening large bivalves requires force, but especially skills. Oystercatchers are specialists, not only in their diet but also in the technique they use to handle the prey (Sutherland *et al.* 1996). Bivalve feeding Oystercatchers can be divided into stabbers, which force their bill between the valves and cut the adductor muscle, and hammers, which smash their bill through one of the valves (Wanink & Zwarts 1996). Amongst these techniques, specialization can be even more refined with individuals concentrating on hammering only the right-hand or left-hand valve of a mussel! Moreover, even amongst individuals within and between populations, different specialized diets and techniques are used. This specialization enables an oystercatcher to exploit a prey that is largely un-utilized by other species and so allow a relatively high foraging efficiency (Hulscher 1996). To open a bivalve, a strong and well-developed bill is necessary. The bill of a juvenile oystercatcher is still not developed well to open a mussel or cockle. Therefore, in the first weeks of an oystercatcher life, a chick has to be fed by its parents, as they are not able to open a bivalve by themselves (Safriel *et al.* 1996).

As the parents open the bivalves in front of the chicks, the chicks consequently adopt the technique used by its parents. Therefore, specialism is passed through on generations. By switching eggs from nests of oystercatchers with different techniques, it is shown that the technique used by young oystercatchers is learned and not inherited (Safriel 1985, Sutherland *et al*. 1996). This contributes to the fact that oystercatchers are specialists; they cannot adopt a technique without first learning it from their parents. Although it suggest a sort of culture among oystercatchers, it is however more complex. Individual oystercatchers have a favoured technique, but they are more flexible than we might think and often use an alternative (Sutherland *et al.* 1996). For example, youngsters that were grown up inland will winter on the mudflats, but they have never learned the techniques to forage on marine preys. Still, most oystercatchers prefer a certain prey and the technique they use to feed on that prey. This specialization can also be distinguished when observing the morphology of the bill of different oystercatchers. Birds that feed on worms have more pointed bills, as birds feeding on bivalves have a more blunted bill because of hammering or stabbing to open the shell (Van de Pol 2006). However, this morphology characteristic is flexible and oystercatchers can change from a pointed into a blunt-bill type in about two weeks as a result of a switch in diet (Van de Pol 2006). Therefore, oystercatchers are not that strict in their diet. Nonetheless, the techniques an oystercatchers uses to prey on bivalves is unique and requires great dedication to learn it.

Habitat change

In the forty years of an (fortunate) oystercatcher' life, many things can change. The Eurasian Oystercatcher population has always been a common shorebird along the beaches and tidal mudflats of Western Europe. In the Netherlands, Oystercatchers mainly occur in the Wadden Sea and the numbers increased or were at least stable until 1990 (Goss-Custard *et al*. 1996). Since 1990 however, the Dutch breeding population declined dramatically with 50 percent and the Dutch Wadden Sea population (breeding and wintering birds) declined with more than 40 percent (fig. 4) (Oosterbeek *et al*. 2006, Van de Pol 2006). This trend concerns the population of Schiermonnikoog too (Bruinzeel 2004, Van de Pol 2006).

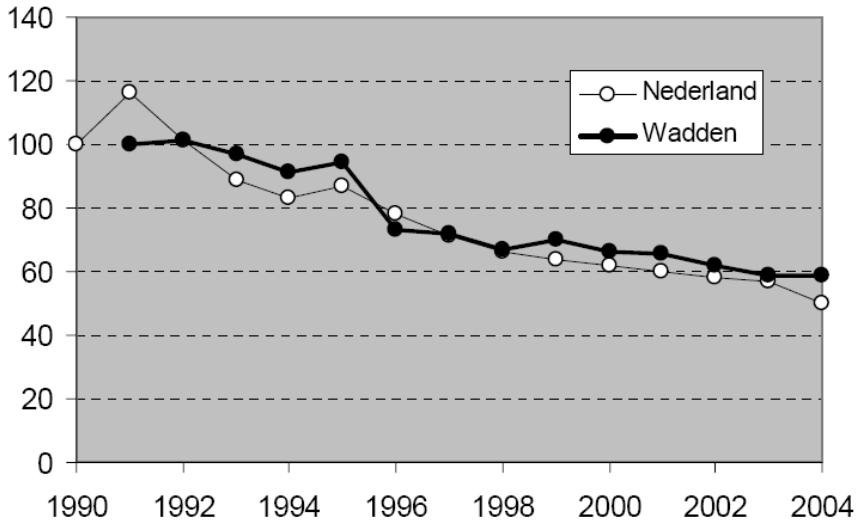


Figure 4: Trend in the numbers of breeding oystercatchers in the Netherlands (white dots) and for the Dutch Wadden Sea (black dots) since 1990. After Oosterbeek *et al.* (2006).

Causes of population decline

As this decline is widespread among Oystercatcher populations, it is likely that one environmental factor such as food availability or weather conditions are the cause of this decline. Food seems most likely, as since 1990 the food conditions deteriorated due to large-scale mechanical shellfish fisheries in the Wadden Sea. These fisheries had a great impact on the benthic fauna by sucking up sedimentation to harvest cockles and they fished away virtually all the natural mussel beds (Piersma *et al.* 2001). Mussel beds are very important for many species and are very rich habitats with high biodiversity (Van de Kam *et al.* 2004). During the winter, oystercatchers forage mainly around mussel beds, as they main preys during that time of the year are cockles and mussels (Hulscher 1996). The loss of the mussel beds and decreasing food availability caused higher mortality rates, resulting in declining numbers of oystercatchers and other species that depends on shellfish such as Eider Ducks (*Somateria mollissima*) and Red Knots (*Calidris canutus*) (Atkinson *et al.* 2010). As 30% of the European Oystercatcher population (including inland breeding birds) winters in the Dutch Wadden Sea (Oosterbeek *et al.* 2006), other populations will also be affected by the deteriorating food conditions in the Wadden Sea.

To protect shellfish eating birds and to restore important habitats, marine protected areas (MPAs) were created in which shellfish fisheries was forbidden (Verhulst *et al.* 2004). Although in 1999, almost one third of the area of intertidal mudflats in the Dutch Wadden Sea was protected and the food availability was higher in those areas, Oystercatchers did not use the areas more than unprotected areas (Verhulst *et al.* 2004). This seems to be strange, especially because mortality is 43% higher outside the MPAs (Verhulst *et al.* 2004). From an Oystercatchers' perspective, it is however more than logic to stay in your familiar feeding territory. This site fidelity avoids the situation that an oystercatcher emigrates to other feeding grounds and encounters worse conditions and competition with local birds. An Oystercatcher is so faithful that it rather dies than leaves its feeding territory. Nonetheless, in severe winters when food is inaccessible in the Wadden Sea, Oystercatchers migrate *en masse* to the Dutch delta or even more south in search for better conditions (Camphuysen *et al.* 1996, Hulscher *et al.* 1996). So ironically, Oystercatchers only migrate when there is suddenly no food accessible, but when food availability slowly decreases they decide to stay. This behaviour was also observed in the Wash estuary (UK) where Oystercatchers not migrated because of low shellfish abundance, but only shifted to alternative foraging methods and prey (Atkinson *et al.* 2010). Large movements of birds because of food shortage are well known and are generally termed as invasions (Gill 2007). Crossbills (*Loxia curvirostra*) for example can migrate thousands of kilometres when coniferous trees in their breeding grounds produced not enough cones, their main food source. Other more site faithful species show only site fidelity when conditions are good. Females Tengmalm's Owls (*Aegolius funereus*) are only site-faithful during vole peaks (from which the numbers fluctuates in a three year cycle) (Löfgren *et al.* 1986). In addition, some Arctic species with high nest site fidelity only breed during vole peaks, such as Snowy Owls (*Bubo scandiacus*) or Arctic Skuas (*Stercorarius parasiticus*). Red Knots face in the Wadden Sea yearly variations in their food sources (small shellfish), and they anticipate on that by using large areas of the Wadden Sea to forage (Spaans *et al.* 2009). For Oystercatchers, this tactic could also be more beneficial than staying at one site, as they are shellfish eaters too.

When in spring temperature rises and other prey will become available, Oystercatchers can forage on worms too to supplement their diet. As I already mentioned, Oystercatchers can change their bill morphology in a rather quick period. However, Van de Pol (2006) observed that the bill morphology changed dramatically over the years. In the whole population and both of males and females, the bill changed from a blunted one that is associated with a diet of shellfish towards a pointed one that is associated with a diet of primarily worms. This showed that shellfish populations are not sufficient anymore to provide the Oystercatchers with enough food and thus they are forced to prey on worms. To meet their energy requirements, an Oystercatcher have to spend more time on the mudflat foraging on worms than it should when it can forages on cockles (Kersten 1996). As they are spending longer times on the mudflat, eggs and chicks have a higher chance to be predated resulting in a decreased egg and chick survival during the last decade (Bruinzeel 2004, Van de Pol 2006). The loss of Oystercatchers' main food, resulted in birds with lower body condition and finally with a lower reproduction success (Verhulst *et al.* 2004, Atkinson *et al.* 2010). Although Oystercatchers can switch to another preys, the deteriorated food conditions will finally result in a further population decline.

Habitat loss

The loss of natural habitats is a big threat to populations worldwide. This is especially the case for species with strong site fidelity. Animals facing habitat loss, can decide to stay and fear reduced survival and/or reproduction, or they can move to other more suitable habitats if available. The latter option, is however not the first one a site-faithful animal chooses. Human induced habitat loss is one of the main causes that populations decline or even extinct nowadays. However, other factors such as weather conditions or increased densities of animals can deteriorate a habitat too. European Storm Petrel (*Hydrobates pelagicus*) populations in France declined over 18 years due to nest site destruction caused by erosion and increasing numbers of Great Cormorants (*Phalacrocorax carbo*) breeding in the colony (Cadiou *et al.* 2010). Rapidly increasing numbers of Lesser Snow Geese (*Chen caerulescens caerulescens*) caused habitat loss in their Arctic breeding grounds due to their own grubbing activities, resulting in Arctic desserts that are unfavourable for breeding (Jefferies & Drent 2006). However, just like the Oystercatcher, many individual geese retain strong fidelity to their nest sites resulting in less fecundity (Ganter & Cooke 1998).

In less than a century, humans have modified natural habitats on large scales. Forests and heath lands were converted into agricultural or urban areas, and especially in the Netherlands large parts of the intertidal mudflats were turned into polders. The tidal area in the Oosterschelde (Dutch Delta) reduced with one-third after the completion of a storm surge barrier and two dams between 1986 and 1987. Affected wader species were first able to settle nearby when the first dams were completed. However, when the largest project was finished the numbers of waders started to decline (Duriez *et al*. 2009). The loss of feeding grounds resulted in more competition between Oystercatchers that were forced to forage on the remained mudflats were other Oystercatchers had their feeding territories (Duriez *et al*. 2009).

Climate change

One of the most discussed issues nowadays is probably climate change, which will have a great impact on biodiversity worldwide. Global temperature rises at a rate much faster than experienced over most of earth's history, and this change is expected to continue in the future (IPCC 2007). This can be especially beneficial for Arctic breeding birds, which are dependent on ice and snow free patches for breeding (Jensen *et al***.** 2008). Warmer winters will also beneficial for Oystercatchers as mortality of Oystercatchers is mainly caused by severe winters (Camphuysen *et al.* 1996). Models even showed that a temperature rise of ~1°C could potentially save the Oystercatcher population from extinction (Van de Pol 2010a). However, for most species global warming would be detrimental. Advancing phenology forces species to move northwards to coincide with food peaks. Especially migratory species have a problem, as their food phenology advances at a faster rate than those birds can adapt too, resulting in a mismatch between food peak and reproduction dates (Both & Visser 2005). In response to global warming, many species advance their time of breeding. Again, the oystercatcher is an exception on this rule. The populations of Schiermonnikoog and Texel increased significantly their date of eggs laying over time (Bruinzeel 2004). As this trend occurred in both populations, a Wadden Sea wide factor is likely to be responsible. Warm winters, will result in less abundance of Oystercatchers' main prey (Van de Pol 2010a). When shellfish stocks are low, adult Oystercatchers will be in low condition when breeding season starts and choose to wait with reproduction. By doing so, they will face another problem caused by climate change. It is

expected that sea level will rise and more extreme events such as flooding will occur (IPCC 2007). Van de Pol *et al*. (2010a) showed that for six bird species breeding on salt marshes in the Wadden Sea area, the risk of flooding increased during the last decades (fig. 5). This coincide with the trend that floods occur more often during the breeding season, especially in May and June. Because Oystercatchers increased their laying date, their clutches have an even greater chance to be washed away.

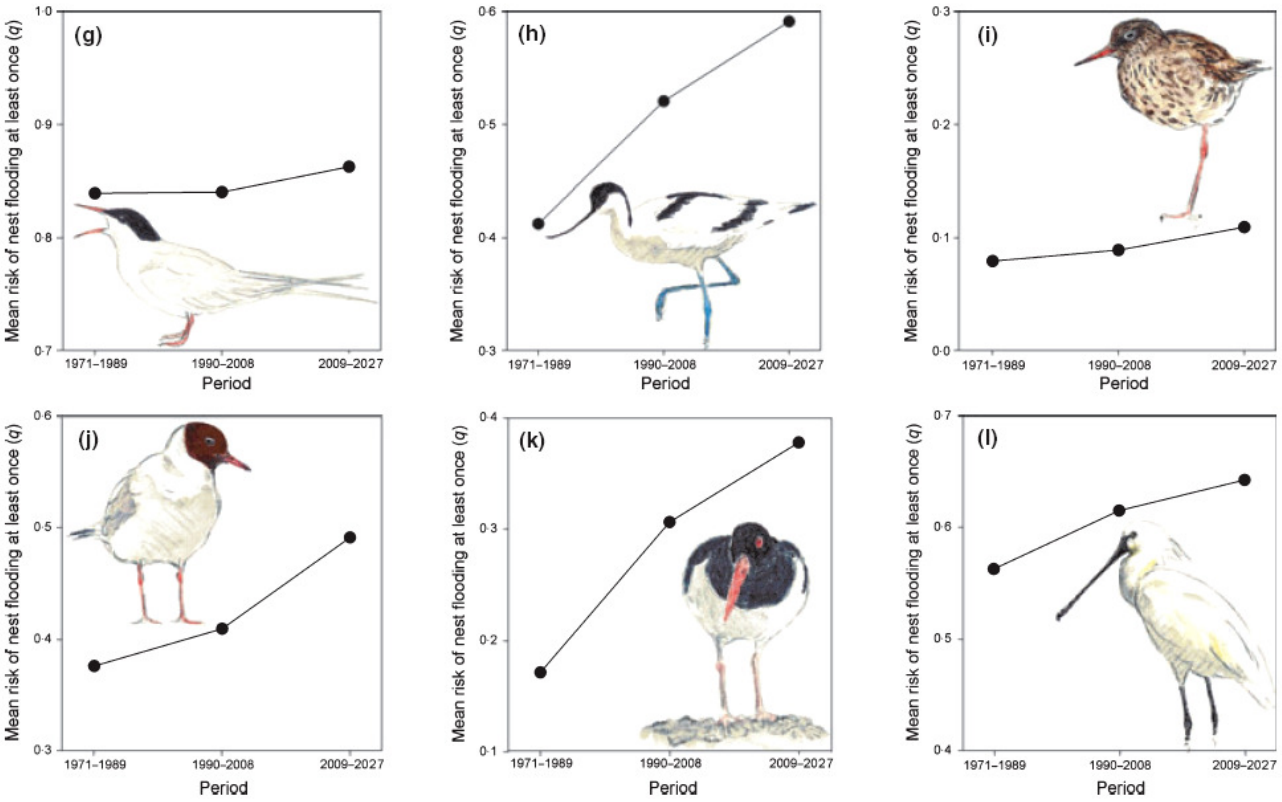
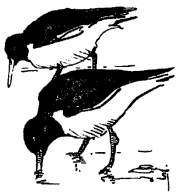


Figure 5: Historical (1971–1989), current (1990–2008) and future (2009–2027) flooding risks averaged over the entire distribution of six bird species: clockwise Common Tern (*Sterna hirundo*), Pied Avocet (*Recuvirostra avocetta*), Common Redshank (*Tringa totanus*), Black-headed Gull (*Larus ridibundus*), Eurasian Oystercatchers (*Haematopus ostralegus*) and Eurasian Spoonbills (*Platalea leucorodia*). Note that y-axes differ in range. After Van de Pol *et al.* (2010a).

Discussion



We can clearly state that Oystercatchers are remarkable birds. Their great dedication to acquire a high quality territory resulted in an even remarkable society in which individuals have to plan their whole career. The decisions they make are quite conservative. Stay where you are is the device and it holds for their nesting, feeding, wintering and roosting sites. Site fidelity is beneficial for these birds to acquire information about an area (e.g. food abundance, social status of other individuals) and to build up local dominance, which is of important for acquiring a territory (Heg 1999). Their territorial behaviour is also to avoid competition. They are filling up a niche by specializing on large shellfish and using their own techniques (Sutherland *et al.* 1996) This specialization might even be the result of their site fidelity by feeding on the most abundant or profitable prey species in their territory.

Imprisoned on the salt marsh

We may conclude that Oystercatchers by being faithful are not very adventurous species. However, to become a successful breeding bird they have to be site faithful and thus site fidelity is eventually advantageous. Moreover, the decision to maintain a feeding site during the winter also pays when food stocks can be reliably predicted according to the available food in the previous years. These decision rules worked perfectly well until man changed the predictability of food stocks between years by removing all food resulting in deteriorating food conditions (Piersma *et al*. 2001). Since 1990, Oystercatchers got in difficulties by being so site faithful. The example that Oystercatchers rather die than migrate to another place when food conditions worsen illustrates this sadly. The Oystercatchers' habitat changed from a rather high quality one with high abundance of food into a low quality habitat. Are we now able to give an answer on the main question: Is site fidelity in Oystercatchers working as an ecological trap? First, I emphasize the definition of an ecological trap again. An ecological trap is when an environment has been altered suddenly by human activities and in which an organism makes a maladaptive habitat choice based on formerly reliable environmental cues, despite the availability of higher quality habitat (Schlaepfer *et al*. 2002).

The first point in this definition is true for the Oystercatcher population of Schiermonnikoog; mechanical fisheries caused a dramatically loss of food within a few years time. The second point, that organisms make a wrong habitat choice based on outdated cues, is also true but more difficult to apply on this Oystercatcher population. Oystercatchers did made a wrong choice to stay in their deteriorating habitats, resulting in a declining population. However, what those cues were that determined their habitat choice is not easy to say and depends on different factors. For feeding territories in winter, the food availability is an important cue. Because food availability decreased and Oystercatchers stayed faithful to their site, we can conclude that those feeding territories are working as an ecological trap. For breeding territories however, many more cues play a role by making the decision to breed somewhere. This has largely to do with the notable Oystercatcher society. Resident territories (high quality) are favoured among non-breeders and the main cue could be the distance of the territory to the mudflats, or the numbers of chicks reared in those territories (non-breeding birds are well informed about the status and quality of the territory they would like to take over

by visiting those territories frequently). If their decision is based on the number of fledglings produced in a territory, than Oystercatchers should choose a breeding site somewhere else as the annual fledgling production decreased to almost zero during the last decades, even for high quality territories (Van de Pol 2006). The large difference in reproduction success between resident and leapfrogs birds described by Ens (1992), has been reduced and resident birds are not that successful anymore (Van de Pol 2006). However, once they are in the race for a breeding territory, it is not easy to quit as they have invested lots of time and energy for many years and have to start all over again when leaving the area. As the average age of an Oystercatcher to acquire a territory is seven (Bruinzeel 2004), between the time an Oystercatchers choose for a certain territory and when they finally acquires it, the quality of that territory can change. Eventually, an Oystercatcher can be saddled with a low quality territory instead of a high quality resulting in lower fitness. When this situation occurs, than we might say that Oystercatchers are 'trapped' by their habitat preferences and thus their great dedication and faithfulness to a specific site works as an ecological trap.

In conclusion, the long time an Oystercatcher has to invest was always beneficial but is probably becoming more and more detrimental if the quality of the territories drops any further. To escape from this 'prison', Oystercatchers have to give up their site faithfulness and migrate to other places. In recent years this seems to be the case, as the emigration rate of adults has increased manifold (fig. 6) (Van de Pol 2006). This trend was also observed in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) from which the males used to show high site fidelity, but in a response to habitat deterioration their site fidelity became weaker (Beletsky & Orians 1994). This reduced site fidelity can turn the negative trend of the Oystercatcher population. Unfortunately, nothing is further from truth. The increased numbers of bird emigrating out the population of Schiermonnikoog will result in a further decline of the population; however the numbers of non-breeding birds remained constant over the years (Van de Pol 2006). Together with the reduced reproduction output of breeding birds and the increased emigration of adults, this would mean that there is also a large part of birds that immigrates into the population on Schiermonnikoog, suggesting that conditions elsewhere are probably even worse.

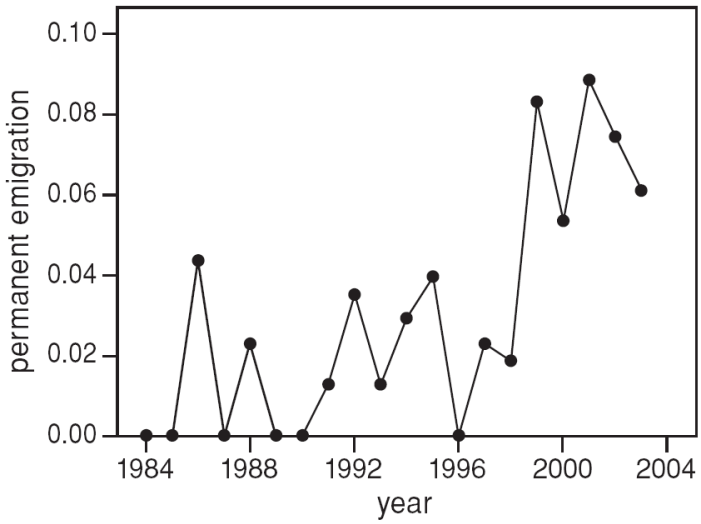


Figure 6: Annual permanent emigration of the Oystercatcher population on Schiermonnikoog. After Van de Pol (2006).

Looking to the future

The future prospects for Oystercatchers are not very bright. If habitat conditions will not improve, an Oystercatcher has to adapt to its novel environment to escape from possible extinction. Selection for new habitats is difficult as habitat selection in birds is partly a genetic trait (Gill 2007). This genetic basis of habitat selection is probably responsible for a slow response by some birds to human changes in the environment (Krebs 2001). Natural selection can also change the habitat preferences, but in a short time span it is only sufficient for short-lived species with large heritable variation in habitat preferences (Kokko & Sutherland 2001). Long-lived species should anticipate on deteriorating conditions by learning. Black-tailed Godwits (*Limosa limosa limosa*) are long-lived species and site faithful. However, they decide to nest close to the previous breeding site only a few days before they start with egg-laying by visiting those sites (Van den Brink *et al.* 2008). Oystercatchers can also learn of failed breeding season and decide to nest somewhere else, but their social system thwarts the Oystercatchers. Some leapfrog birds are able to take over a resident territory, but only if there is an opportunity to do so (Bruinzeel 2004). For resident birds, the costs of abandoning your mate and territory are probably too high and too risky.

The miserable situation of the Oystercatcher can only change when food conditions improve in the Wadden Sea. Since 2005, mechanical shellfish fisheries are prohibited in the Wadden Sea and there are some recoveries of mussel beds in the eastern part, nevertheless recovery of the food situation will probably take decades (Kloff & Reneerkens 2006). Furthermore, the predicted increase of severe floods caused by climate change can be another problem (Van de Pol *et al.* 2010a). In conclusion, the strong site fidelity of Oystercatchers caused them to live in a deteriorating habitat resulting in a declining population. That strong site fidelity is the result of their territoriality and monogamy, but above all, it is the result of their social system, which forces Oystercatchers to be site faithful to become a successful breeder eventually. Among other species, Oystercatchers are on many aspects unique. And sadly enough, their unique and strictly behaviour makes them also vulnerable to become entrapped in their 'preferred' habitats.

Jeroen Onrust

s1727605
J.Onrust@student.rug.nl

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Summary

In this thesis I will discuss whether site fidelity in Oystercatchers is working as an ecological trap. The population of Oystercatchers (*Heamatopus ostralegus*) in the Netherlands declined dramatically during the last two decades as a result of deteriorating food conditions in the Dutch Wadden Sea. Oystercatchers are highly territorial and show strong site fidelity which is the tendency to return to a previously occupied location. Site fidelity may be favoured because long-term familiarity with a territory and its surroundings should lead to increased individual survival and higher fitness. Returning annually to the same site avoid the costs associated with searching for new breeding sites and mates. Many bird species show site fidelity, not only for nesting sites but also for staging and wintering sites. Site faithful birds are often monogamous and form a pair bond for a certain time period. A nesting site can work as a meeting point for these birds when separated in the non-breeding period. Birds have a higher tendency to return to a previous breeding location if the breeding success of that year was high. The difference in habitat quality results in birds competing for high quality territories.

On the island of Schiermonnikoog in the Dutch Wadden Sea, this difference in habitat quality resulted in a population with birds breeding in low and high quality territories. The difference is based on the distance of the nesting territory to the mudflats. High quality territories have an adjacent feeding territory, which is advantageous because Oystercatchers are semi-precocial and thus can take their chicks to the mudflats. Birds breeding in low quality territories by contrast, have to commute between the nesting on the salt marsh and feeding territory on the mudflats to provide their chicks with food. As a result, birds breeding in high quality produce on average more offspring. As high quality territories are scarce, Oystercatchers have to compete for it. To acquire a territory a non-breeding bird has to build up local dominance which increased their chance to eventually take over a territory. Building up local dominance, force the birds to stay where they are and it can take quite some years to finally become a breeding bird.

Oystercatchers are specialized feeders and feed mainly on shellfish. Since 1990, almost all shellfish was fished away by mechanical shellfish fisheries in the Wadden Sea. This caused the decline of shellfish eating birds, including the Oystercatcher. Climate change is another problem for coastal breeding birds as the risk of flooding increased. The habitat of oystercatchers deteriorated in the last two decades, nonetheless Oystercatchers decided to stay in that habitat because of their site fidelity. Consequently, this site fidelity works as an ecological trap. An ecological trap occurs when a bird chooses to stay in low quality habitat although high quality territories are available. Oystercatchers decide to stay because their social system forces them to do so, and leaving would be detrimental as they have to build up local dominance all over again. Only if food conditions and thus habitat quality will improve, Oystercatchers can be saved from further decline.

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