rijksuniversiteit groningen

Environmental factors influencing nest site fidelity

in migratory and residential birds

Nathalie Horsting 1884948
Supervisor: Prof. dr. B.I. Tieleman
Animal Ecology
July 2012

Abstract

Some birds breed at the same location every year, some birds change sites a lot. Movement between the first breeding site or group and other groups or sites is called breeding dispersal. This breeding dispersal is dependent on the nest site fidelity. In this thesis I try to answer the following questions: ***In what way do environmental factors influence the nest site fidelity of birds? Is there a difference in these influences between migratory birds and resident (non-migratory) birds?*** I try to to distinguish which factors are for birds the most important factors in breeding dispersal, while looking at food, interspecific competition, intraspecific competition and mate fidelity. In the end I have to conclude that dispersal depends on a combination of environmental en non-environmental factors and it depends on the species and the circumstances which factors are more important. I suggest reasons why I cannot draw any specific conclusions and I suggest that to get more detail on these processes research should be broader. Not look at one factor but examine more factors influencing one species, one population. If the same type of research is done on several species, one could draw better conclusions on general patterns, like comparing migratory and residential species.

Index

Introduction

Some birds breed at the same location every year, some birds change sites a lot (Greenwood *et al.* 1979). Movement between the first breeding site or group and other groups or sites is called breeding dispersal. This breeding dispersal is dependent on the nest site fidelity (Greenwood *et al.* 1979).

Why is it important to know the fidelity of birds? If one knows what influences the fidelity of birds, one can predict the breeding dispersal. Breeding dispersal is important for breeding success, gene flow, genetic structure, population size and evolutionary change (Paradis *et al*. 1998; Greenwood & Harvey, 1982; Wright, 1940; 1943; 1946). When a bird breeds at the same spot as the previous breeding attempt, it might have the benefits of having experience. It might be familiar with the local food resources, the high quality nesting sites and the local predation pressure. The chance of mating with the same partner might also increases. Moving to another spot may have better food resources or less predation (Thorup, 1999). Restrictions on the movements may increase the chance of inbreeding and genetic differentiation of neighbouring groups, and might cause a decline in the population (Wright, 1943; 1946). This is useful information for example for conservation purposes. If a migratory bird wants to breed at the same site as last year, it has to travel back to this area. While travelling, it could easily go to a place where the conditions might be better. A resident bird is still relatively close to the area where it has been breeding last year. This makes it easier to get back to the site and makes it more effort to go to a new place. This might result in a difference between the two types of birds. But is this true, does this happen in real life? Is there a difference between the nest site fidelity of migratory birds and the nest site fidelity of resident birds?

In this thesis I define migration as an annual, seasonal movement of birds. Migratory birds breed in one place and winter at an other place. Resident birds stay at about the same area all year and do not winter at a different place as the breeding area..

There are several factors that could have an effect on the fidelity of birds to their breeding site. Part of these factors are environmental. This is the focus of this paper. Environmental factors include predators, food en the social environment, like mate fidelity and competition. Factors like sex also have an influence on the nest site fidelity. Sex is not an environmental factor, but it has a lot of influence on the importance of environmental factors: reasons to disperse can be different for males and females. This is why I cannot exclude sex from my story.

The central questions in this thesis are:

In what way do environmental factors influence the nest site fidelity of birds? Is there a difference in these influences between migratory birds and resident (non-migratory) birds?

The environmental factors I am discussing can be split up in several 3 groups of factors. These are:

- food
- predation, interspecific competition
- social factors: intraspecific competition, mate fidelity

Food

If the abundance of food is low, birds might not be able to feed themselves and/or their chicks, which lowers the breeding success and could even mean death of one or both parents. This could mean that it is a factor in whether to move or to stay (Greig-Smith, 1982). I expect food abundance to be an important factor in both migratory and resident birds, because every bird needs enough food to raise a brood and stay alive themselves. Successful rearing of offspring may reduce the food available for subsequent broods, which could make it beneficial to move away from the area (Greig-Smith, 1982). If the carrying capacity of an area is not high enough, and the lack of food becomes too severe, I expect every bird to be forced to move.

Examples of birds who are indeed influenced by this are the common crossbill, *Loxia curvirostra*, the evening grosbeak, *Hesperiphona vespertina*, the Siberian nutcracker, *Nucifraga caryocatactes* and the Clark's nutcracker, *Nucifraga columbiana* (Greenwood & Harvey, 1982). They are resident birds, who stay in the same area when food is abundant. However, when a seed-crop failure occurs, they emigrate to places with better food resources, especially when the population density is high (after a productive breeding season) (Greenwood & Harvey, 1982). Species who feed on tree seeds are generally more affected by food depletion than species who feed on other temperate plants. This is because tree seeds tend to fluctuate more (Newton, 1972). Some birds do return to the original breeding site, but others remain to breed in the new area, with high food abundance (Svardson, 1957; Vander Wall *et al.* 1981). Not only the breeding site fidelity of seed eaters is influenced by the abundance of food. Also birds of prey that feed on cyclic populations of rodents move to places with higher food abundance when the densities of small mammals are low in their current area. The places with higher food abundance are places where the population cycle is out of phase with their original breeding place. Examples of this are the snowy owl, *Nyctea scandiaca* (Lack, 1954), and the rough-legged hawk, *Buteo lagopus* (Galushin, 1974). Some snowy owls are resident, some are migratory. The Rough-legged hawk is a migratory species. The stonechat from East Sussex, UK, *Saxicola rubicola*, a resident bird who feeds on insects, also disperses further when the food resources become less (Greig-Smith, 1982).

Although some species do have a high(er) breeding dispersal when food abundance is low, most species don't respond to the low abundance by moving away (Greenwood & Harvey, 1982). Examples of this are the albatrosses, *Diomedeidea* (Fisher, 1971), which are resident birds, and gulls and terns, *laridae*, who are migratory (Austin, 1949; Chabrzyk & Coulson, 1976; Mills, 1973; Vermeer, 1963; Wooller & Coulson, 1977). But not only seabirds show this behaviour. Also passerine birds like the great tit, *Parus major* (Bulmer, 1973; Dhondt & Huble, 1968; Greenwood *et al.* 1979; Harvey *et al.* 1979), pied flycatcher, *Ficedula hypoleuca* (Berndt & Sternberg, 1969; Haartmann, 1979), and the song sparrow, *Melospiza melodia* (Nice, 1937;1943), show high nest site fidelity, even when the food abundance is low. The great tit and the song sparrow are residential birds, the pied flycatcher is migratory. Another example of a migratory bird who generally does not adjust its nest site fidelity to a declining food abundance is the piping plover, *Chradrius melodus* (Haig & Oring, 1988).

The piping plovers tend to have a high breeding site fidelity (table 1) (Haig & Oring, 1988). Territories that are abandoned by a pair, are immediately inhabited by a new pair, that usually stays for the remainder of the breeding season. This indicates that resource depletion is rarely a reason for piping plovers to leave a breeding site (Haig & Oring, 1988). They forage not only on their territories, but also outside the territory, which makes the birds less dependent on the food abundance on the territory itself (Haig & Oring, 1988). Although many bird species are less likely to return to an area after poor breeding success in an area (Martin, 1974; Darley *et al*. 1977; Brooke, 1978; Harvey *et al.* 1979; Oring & Lank, 1982; Oring *et al.* 1983; Blockstein, 1986; Weatherhead & Boak, 1986), piping plovers tend to return to their previous site, regardless of previous success or failure (Wiens, 1986). The birds have to cope with a lack of suitable nest sites, which is indicated by the decreasing amount of nesting sites and large amount of non-breeding birds at for example West Shoal Lake (Wiens, 1986; Haig & Oring, 1987). When local population densities are high, or suitable nesting sites are scarce, birds may be more successful if they returns to a familiar area than if they move elsewhere (Weatherhead & Boak, 1986).

Previous success	Percentage return		
	Males	Females	Overall
Chicks hatched	73.3 (15)	54.5 (11)	65.4 (26)
Nests failed	76.5 (17)	57.1 (14)	67.7 (31)

Tab. 1. Breeding site fidelity of Piping Plovers in southern Manitoba by previous year's reproductive success. Sample sizes (in parentheses) are the number of individuals monitored. (Haig & Oring, 1988)

The Stonechats from East Sussex, UK, tend to move further within a year after having successfully raised chicks at their previous nest. The weight of stonechat nestlings are greater at greater distances from the previous nest (fig. 1). This could be explained by progressive food depletion around the nest when the chicks are fed. The larger the previous brood, the larger the benefits of moving (further) away. This also accounts for the high growing rates near to previous nests that had failed to fledge any chicks (fig. 1) (Greig-Smith, 1982). The food supply for the birds is constantly renewed throughout the breeding season, as new taxa emerge (Eagles, 1977; Bibby, 1979), but the diet of the nestlings is heavily dependent on only a few large-bodied taxa, such as sawfly larvae (Gibb & Betts, 1963; Royama, 1970, Pinkowski, 1978; Maher, 1979), that are relatively easy to find and are therefore easily depleted (Greig-Smith, 1982).

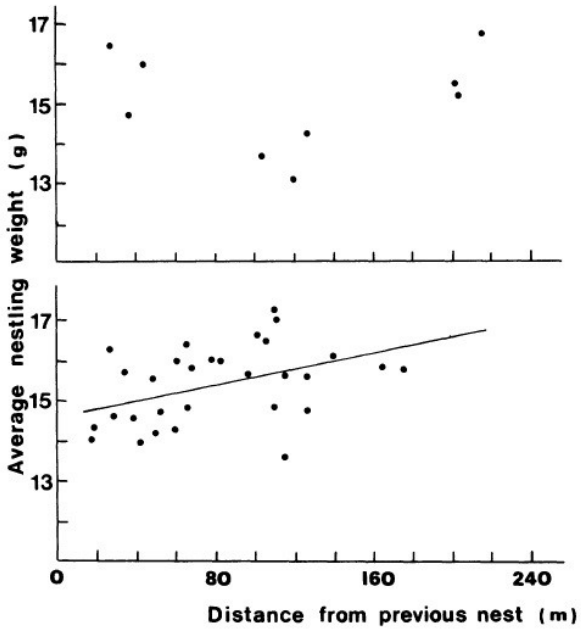

Fig. 1. Growth of Stonechat nestlings, measured as average weight on days 9-13, in relation to distance from the previous nest site. Each point represents the average for one brood, divided into broods following (a) no young, (b) two to six young fledged from the previous nest (Greig-Smith, 1982).

So, in both migratory and residential birds, one can find species that move away from their nest site when food abundance becomes low and species that don't adjust their site-fidelity to the (relative) abundance of food.

Predation

A lot of birds loose their clutch to a predator, some species up to 40% overall (Porneluzi, 2003; Haig & Oring, 1988). In the willow ptarmigan, *Lagopus lagopus*, up to 86% of the first clutches gets predated (Hannon *et al.* 1988). If a bird's nest gets predated, this means their breeding attempt has failed and they either have to start over this year, or wait another year and try again next breeding season. It could be saver for a bird to move away from the predated nest, to lower the chances of getting predated again. The predator might remember the nest site and search there again for easy prey. This, in combination with the high percentages of predation in a number of birds, is why I expect predation to be a very important factor in site fidelity of birds. Both migratory and residential birds can get their nests predated, so I do not think there will be a big difference between the two.

If the predator species is patchily distributed over the area, moving away from a site where the nest has been predated might decrease the chance of the birds nest getting predated again. However, if the predators are universally distributed, moving away does not necessarily decrease the chance of predation (Rohwer, 1983). The latter is the case with piping plovers, *Charadrius melodus*, (migratory) in Manitoba. Predation of the nest does not make piping plovers change site a lot. They remain mainly on their territories and the new nest site will be within 30 meters of the previous ones. Their territories tend to be clumped, so if they move to another territory in the same area, this would not decrease the chances of being predated again (Haig & Oring, 1988).

Willow ptarmigans, *Lagopus lagopus,* who are also migratory, experience most of their reproductive failure because of clutch predation. Their predators show area-concentrated search patterns, which could make it useful to switch territories to avoid predation. The female willow ptarmigans however, do not switch sites after being predated. Clutch predation is variable and unpredictable in this case and the hens have higher loss of clutches after switching than before. This makes it less attractive to switch sites (Schieck & Hannon, 1989).

In some species predation has a small influence, but is not the most important factor in breeding dispersal. This is the case in the stonechat, *Saxicola rubicola*, from East Sussex, UK, a resident bird (Greig-Smith, 1982). Also the sparrowhawk (migratory), *Accipiter nisus* (Newton & Marquiss, 1982), and the wheatear (some migratory, some resident), *Oenanthe oenanthe* (Brooke, 1979), are more affected by other factors. They tend to chance sites more often because of differences in territory quality than predation (Greenwood & Harvey, 1982).

There are cases where migratory birds do show dispersal behaviour after predation on their nest. The reed warbler, *Acrocephalus scirpaceus,* for example, does disperse more after predation (Catchpole, 1972). More examples of migratory birds dispersing after predation are the pied flycatcher, *Ficedula hypoleuca* (Haartmann, 1979) and the ovenbirds, *Seiurus aurocapillus* (Porneluzi, 2003).

In ovenbirds, *Seiurus aurocapillus*, like many other species, predation is the primary reason for nest failure (Greenwood & Harvey, 1982; Drilling & Thompson, 1988; Bollinger & Gravin, 1989; Porneluzi & Faaborg, 1999). The dominant nest predators of the ovenbirds are the American crow, *Corvus brachyrhynchos,* the blue jay, *Cyanocitta cristata,* the raccoon, *Procyon lotor,* and the opossum, *Didelphis virginiana* (Porneluzi, 2003). These predators often stay in the same area for several years and forage in the same areas if they are successful there (Porneluzi, 2003). This means, that an ovenbird territory that has been predated in one year, has a higher chance of predation the following year. This makes it more beneficial for an ovenbird to move after predation, to lower the risk of getting predated again. This is also found in the behaviour of the male ovenbirds. Successful and unpaired males return to the same location rather than to disperse to a unfamiliar site (fig. 2) (Bayne & Hobson, 2001; Porneluzi, 2003). The return date of unpaired and successful male ovenbirds (48%) is similar to the estimates of annual survival for ovenbirds (60%) (Faaborg & Arendt, 1995; Porneluzi & Faaborg, 1999). The return rate of the paired, unsuccessful males is much lower (fig. 2). This indicates that predation is indeed a very important factor in the dispersion and nest site fidelity of ovenbirds.

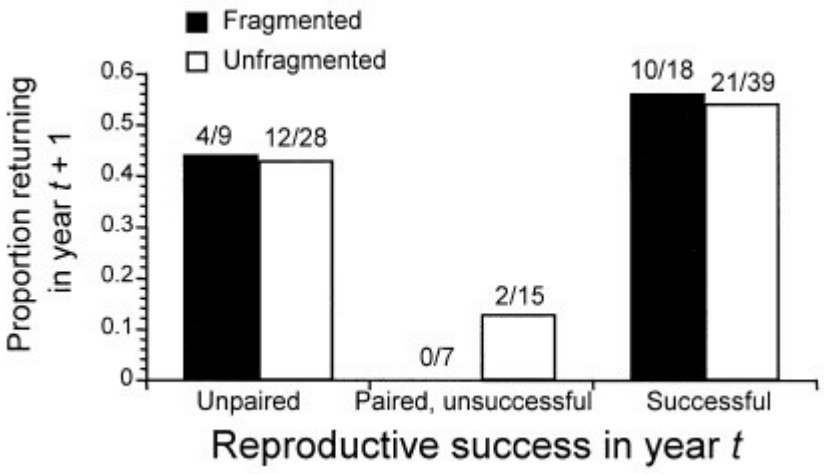

Fig. 2. Proportion of male Ovenbirds returning in year t + 1, grouped by their reproductive success in year t, for fragmented and unfragmented landscapes in Missouri. Males settling more than 200 meters from their previous territory would not have been observed and were classified as not returning. (Porneluzi, 2003)

In the stonechat (East Sussex, UK), *Saxicola rubicola*, a resident bird, predation has a small influence on their movement within a year, but is not the most important factor in breeding dispersal. Their nests are even more likely to fail when a bird moves a long distance from their previous nests (long distance means > 175 meters). Data indicates that this is largely due to predation (tab. 2), but it is not quite significant. The birds tend to move small distances (fig. 3) (Greig-Smith, 1982).

Distance from previous nest (m)	Number of nests	Number (and %) attacked by predators
1–50	19	3 (15.8)
51–100	17	2 (11.8)
101–150	19	2 (10.5)
151–200	3	1 (33.3)
201–250	8	3 (37.5)

Tab. 2. Predation on Stonechat nests in relation to the distance moved from the previous nest. (Greig-Smith, 1982)

The higher chance of predation at larger distances from the nest (tab. 2) might be the result of the birds moving out of their familiar range, but half of the birds foraging occurs further away from the nest than 125 meters, which makes it a less likely reason. A more likely reason is that far dispersal often leads to the next nest within a year being placed near to wood harbouring predators, because of the size of the habitat patches in this study. (Greig-Smith, 1982)

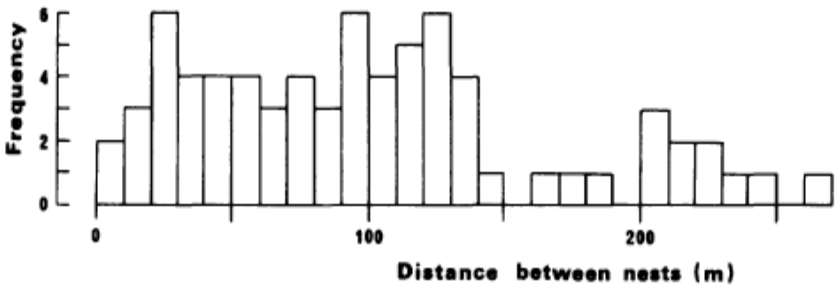

Fig. 3. Frequency distribution of the distances between successive stonechat nest sites (Greig-Smith, 1982)

There is no correlation between the time a nest survives and the distance moved from the previous nest site, which suggests that there is no added risk in remaining close to the previous nest site. After being predated there is an equally high risk of getting predated the attempt. Large broods could draw a lot of attention, which could increase the risks of predation. But there is also an equally high risk of getting predated for nests with large broods. There is therefore no evidence that the risk of predation was increased by predation of the previous nest, or by rearing a large brood. Still, the birds tend to move away further after their nest is predated (fig. 4), which implies that the stonechat follows the common tactic of moving away from areas where predation had occurred. This is unexpected, since the risk of getting predated is not higher after being predated. One factor that could explain this is change of vegetation in which the nest is concealed. This is more likely after predation (fig. 5). It could help to reduce the searching success of a predator, if it searches sites similar to the previous nest. (Greigh-Smith, 1982)

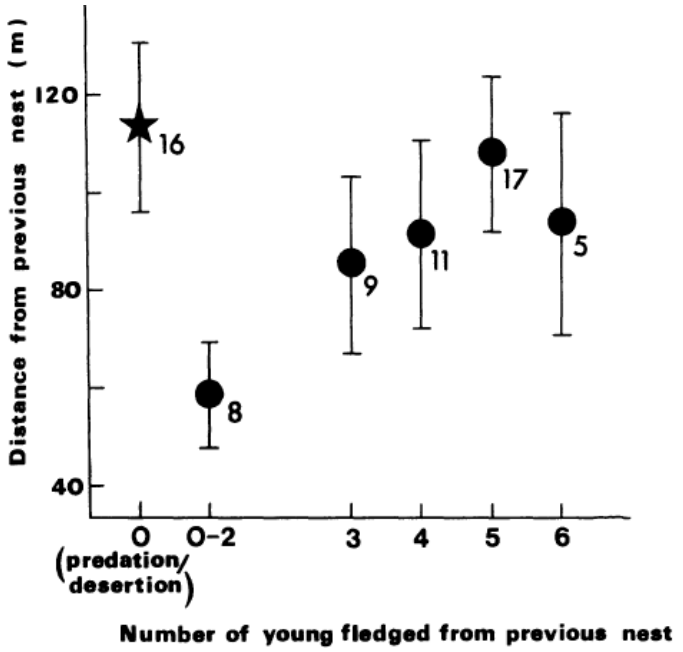

Fig. 4. Average distance moved by stonechats from their previous nest site (mean ±S.E.) in relation to the number of young fledged from that nest (Greig-Smith, 1982)

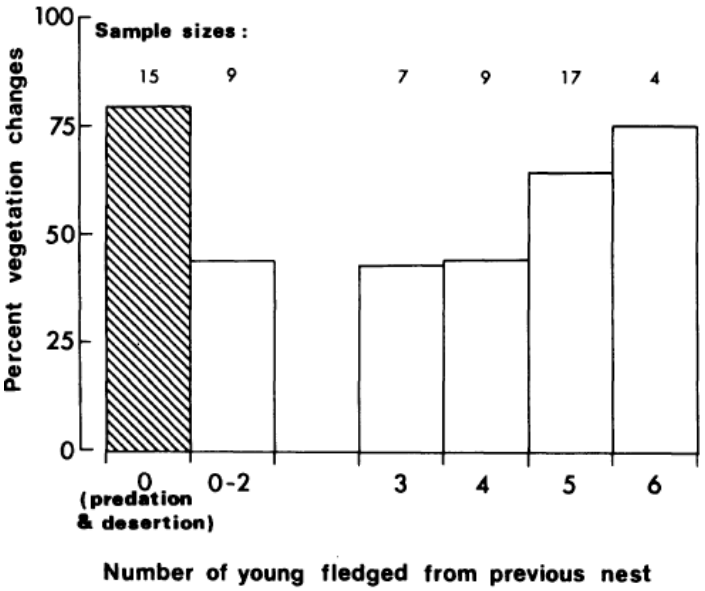

Fig. 5. Frequency with which Stonechats nested in a different type of vegetation to that used for their previous nest, in relation to the number of young fledged from the previous nest (Greig-Smith, 1982)

To piping plovers, who do not tend to change sites after predation, another factor, storms, is more important. 63.8% of the piping plover nests is destroyed: 23.8% by storms, 40% by predation by skunks *(Mephitis mephitis)* and red foxes *(Vulpes vulpes)*. 71% of the breeding adults who survive returns to their previous breeding site the next year. There is no significant difference in males and females in this returning, nor if the nest hatched or failed (tab. 1). The source of the nest destruction makes a significant difference in whether the piping plovers change territories or not. The birds whose nest has been destroyed by a storm are more likely to change territories and move significantly further than those whose nest has been predated. There is no significant difference in reproductive success among birds that change territories after predation compared with those who stay on their territory. (Haig & Oring, 1988) The time involved in dispersal after the nest has been predated, may not be compensated for by the potential benefits from reduction in probability of getting predated again (Wunderle, 1984).

Residential birds also show the pattern of moving away after predation. An example of this is the great tit, *Parus major*. The great tit tends to change breeding sites if the nest has been predated. The female great tits move a significantly shorter distance after a successful brood, than after a brood that has been predated (fig. 6) (Harvey *et al.* 1979).

61% of the successful great tit females move less than 100 meters. Of the broods that are prayed upon, only 40% moves less than 100 meters. Even if the next breeding attempt is successful, the female still tends to breed in another area the following year (Harvey *et al.* 1979). Birds who have been unsuccessful the first time move significantly less within a year than between years. This could be because their dispersal within a year is limited by territory boundaries. Even if the second attempt in the same year is successful, they move the same distance the next year, compared to birds who have no successful brood at all. Successful breeders that stay within 50 meters of their previous nest site are more likely to return to the same nest box than birds that stay within 50 meters if which the nest box was predated. Not only the females move significantly more after their nest has been preyed upon, also males show this difference (Harvey *et al.* 1979).

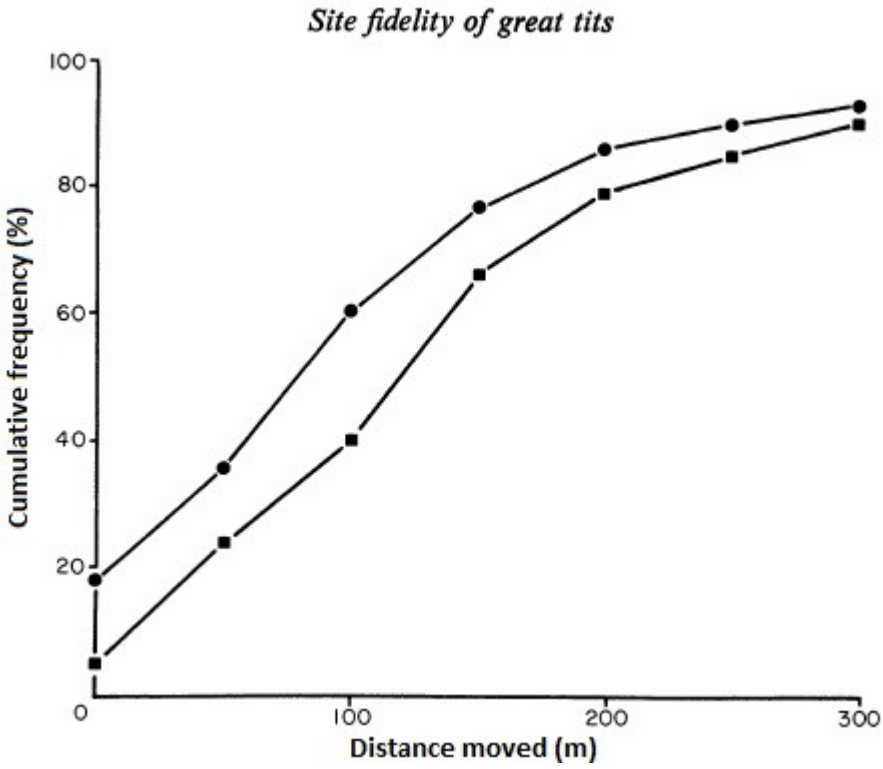

Fig. 6 . Cumulative frequency plotted against breeding dispersal for females moving between years whose last attempted brood was successful (●) and preyed upon (▪) (Harvey et al. 1979)

Predation seems to be an important factor for both migratory and residential birds, but in some species other factors are clearly more important (e.g. storms for stonechats).

Competition for nesting site

In both migratory and residential bird-populations, every year new birds are added to an area. Some of them are older birds who are looking for a new territory, others are born in the area and are trying to find a first breeding site or territory. The space within an area and the resources are limited, causing competition for (good) nesting sites within a species, but also between birds or different species (Greenwood & Harvey, 1982). I expect competition to be an important factor in both residential and migratory birds, because of the previous reasons. I think migratory species experience more competition, because they have to return to the area and (re)occupy a territory before the others do, while residential birds are close to the area, and can time exactly when to return to the territory.

Younger individuals of a species disperse in general more, or occupy territories of poorer quality than the older individuals. The site a new breeder occupies depends on the behaviour of the other, previous breeders, particularly in migratory species. These previous breeders reach the nesting area sooner and can occupy the higher quality sites. The least successful individuals and the younger ones may only be able to occupy a suboptimal area. This can cause the males that remain unpaired. Some individuals do not occupy a territory at all (Greenwood & Harvey, 1982; Hilden, 1979; Brooke, 1979).

In the Temminck's stint, Calidris temminckii, when males become older, they attempt and often succeed in occupying a new, better site (Hilden, 1979). In wheatears, *Oenanthe oenanthe,* the older males arrive earlier than the younger males and are therefore able to occupy the higher quality territories, which means better foraging conditions for females. As the males become older, they tend to change site to higher quality territories. The older males (2 years or older) mostly occupy popular territories, while the younger males tend to occupy the territories that are not that popular. Popularity means whether they are occupied every year or not (tab. 3). (Brooke, 1979)

In this species, it is not clear whether females choose sites as a result of differences in age, quality of males, quality of the territories or the size of the territories (Brooke, 1982). The Temminck's stint and wheatears are both migratory birds.

Age of male	Number of years territory used for breeding in period 1974–76	
	Once or twice	Three times
Two years old/older	3	10
First summer	7	3

Fisher Exact test, $P = 0{\cdot}040$.

Tab. 3. The age of wheatear males occupying territories that were used for breeding once or twice, or three times in the period 1974-1976 (Brooke, 1979)

Not only males compete for nesting sites. In the goldeneye, *Clangula clangula,* also migratory, competition between females for nest sites influences breeding dispersal. This is in interaction with other factors, like avoidance of intraspecific brood parasitism (Dow, 1982).

But not only migratory birds show this behaviour. In eastern bluebirds, *Sialia sialis,* a mostly residential species, the younger males are often forced by the older males to move to more distant breeding areas. The older ones are more familiar with the breeding grounds and this makes them more capable to exploit previous nest sites (Ingold, 1996). In great tits, *Parus major*, in years with a high population density, young males disperse a greater number of territories compared with years with a

lower population density (Greenwood *et al.* 1979). When the density is high, there are more young males looking for territories and more adults returning to the breeding-area. Also the fledging time influences the dispersal. Great tits that leave the nest later during the breeding season tend to disperse further than those birds that fledge early. The late fledgers have to compete not only with the adults, but also with the early fledged young. These early fledged young are heavier and have time and weight in their favour (Greenwood & Harvey, 1982; Dhondt & Huble, 1968). Both cases are natal dispersal, but there could be a possibility that the trend continues after the first nesting attempt, but no research is done on this topic yet.

In the migratory collared flycatchers, *Ficedula albicollis,* young males have to compete with other species for nest holes. Sometimes great tits, *Parus major,* and Blue tits, *Parus caeruleum,* occupy nest holes before the collared flycatchers can return to them. This forces the collared flycatcher to disperse, in order to breed. Great tits and blue tits are both residential birds, what gives them the opportunity to occupy the nest-holes before the migratory collared flycatcher returns from its wintering place. The nest box fidelity of collared flycatchers is quite low, but still the great tit and blue tit makes them disperse even more (Pärt & Gustafsson, 1989).

If within a species the territorial males return earlier than the females, they must compete with members of the same species for breeding resources. An example of this is the hooded warbler, *Setophaga citrina,* a migratory bird. When the hooded warbler population in a breeding site is dense, there is a high competition between females for territories and mates. The costs of searching for a former mate and the costs of competing for former territory could in this case outweigh the benefits of getting them back (Howlett & Stutchbury, 2003).

Some birds do not move larger distances when they have to compete with other species. Red-bellied woodpeckers (resident) have a very high nest site fidelity. They have to compete extensively with starlings for nest cavities, but this seems to have little effect on their nest site fidelity. They still tend to return and nest in the same tree or in trees nearby during the consecutive years (Ingold, 1989;1991).

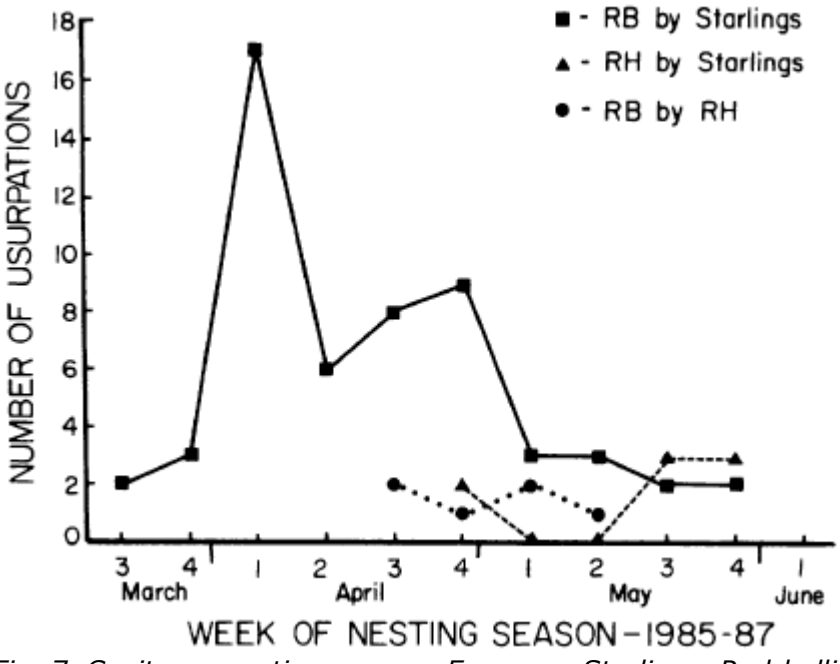

Fig. 7. Cavity usurpations among European Starlings, Red-bellied (RB) Woodpeckers, and Red-headed (RH) Woodpeckers during 1985-1987 (Ingold, 1989).

Red-bellied woodpeckers encounter a lot of competition for nest cavities. About half of the freshly excavated red-bellied woodpecker nest cavities are usurped by starlings. About half of that occurs before the first of May, when both species are initiating nesting (fig. 7). A few occur at the end of May, when the starlings try their last attempts to initiate a nest. But the red-bellied woodpeckers do not only loose their nest cavities to starlings.

They also loose their nest cavities as a result of competitive encounters with red-headed woodpeckers (fig. 7) (Ingold, 1989). 80% of the red-bellied woodpeckers who encountered competition with starlings or red-headed woodpeckers return to the same tree for the next nesting attempt. At least 62% of the red-bellied woodpecker pairs that encounter competition of starlings or red-headed woodpeckers still manages to rear first broods in the same breeding season (Ingold, 1989).

The dispersal of female collared flycatchers is on average further that the dispersal of male collared flycatchers (fig. 8). Only 8% of the males and 2% of the females reoccupies their previous nest box, but most individuals stay within the nest box area: the average distance between occupied nest boxes within a year is 42-61 meters (depending on breeding density for the year and nest box area). Collared flycatchers have to compete for nest holes with early breeding great tits and blue tits (Gustafsson, 1987). Female collared flycatcher dispersal is not significantly affected by this competition, within or between years (tab. 4). Young males however, move significantly further away from their previous nest box if this nest box is occupied by tits (tab. 4).

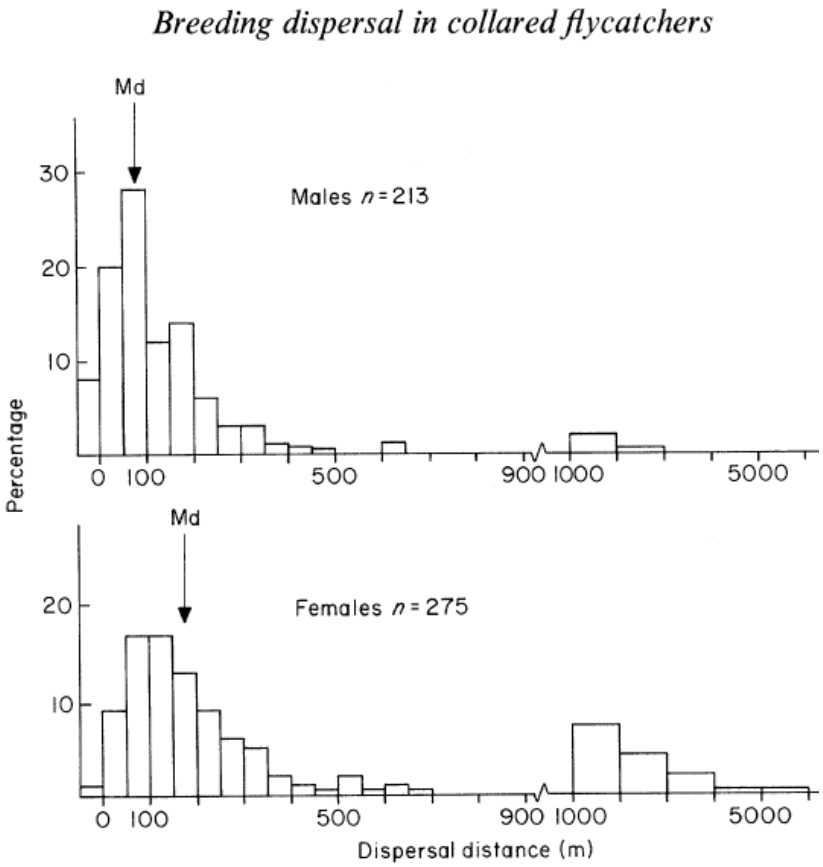

Fig. 8. Breeding dispersal distance (m) for males and females. Birds which have moved over 900 m have shifted nest box area. (Pärt & Gustafsson, 1989)

Category of bird	N	Dispersal distance within nest box areas (%) 0–50	51–100	101–150	151–200	201–250	251–300	301–900	Median	Number of individuals shifting area: Same	Shift
Males											
Old, O	34	20	41	9	20	6	3	0	89·0	45	1
Old, V	81	33	28	11	11	6	1	9	89·0	99	4
Young, O	28	18	25	4	29	11	7	7	158·0	33	0
Young, V	95	30	30	17	13	4	3	3	81·0	101	2
Females											
Old, O	32	12	19	22	22	6	6	12	144·0	41	2
Old, V	83	10	20	23	16	12	7	12	144·0	96	14
Young, O	15	7	20	20	13	20	13	7	179·0	21	3
Young, V	70	14	20	16	16	7	7	20	150·0	101	23

Tab. 4. Breeding dispersal distance of individuals whose previous nest box was vacant (V) or occupied (O) by breeding tits (Pärt & Gustafsson, 1989)

The dispersal of older males is not affected by nest box occupation by tits (tab. 4). Other factors might be more important in their situation, like experience with a certain area. (Pärt & Gustafsson, 1989)

Collared flycatchers have a relatively low degree of site-fidelity, compared to other bird species (Harvey *et al.* 1979; Lawn 1982; Beletsky & Orians, 1987). Since the site fidelity is still low when there is no competition between tits and flycatchers, there should be an other factor involved. This could be the high number of nest boxes, which makes it less costly for individuals to search for alternative sites (Searcy, 1979; Greenwood, 1980; Weatherhead & Boak, 1986). In pied flycatchers this had been shown in experiments, as females were more selective at high nest box densities than at low densities (Alatalo *et al.* 1988). This could also be the case in collared flycatchers, but it has not been proven (yet) (Pärt & Gustafsson, 1989).

In most species competitions seems to be having a significant effect on the fidelity and breeding dispersal of birds. Both males and females can encounter competition. However, there are also species who do not really get affected by competition. Other (environmental) factors might be of more importance.

Mate fidelity

Pairing with a previous partner is thought to give a bird the opportunity to establish a territory and breed early, which could increase their reproductive success. The more seasons the pair is together, the more benefits (Schieck & Hannon, 1989). I think this is true for both migratory and residential birds, however, I do think it is less easy for migratory bird to find their mate after returning to the breeding area then residential birds, because residential birds can be close together during the winter, while migratory birds can loose each other in flight, have to cope with fluctuations in arrival times or do not go to the same area to winter (Soikkeli, 1967; Holmes, 1971; Coulson & Thomas, 1983; Rowley, 1983; Eliason, 1986). So I think that this is an important factor for both migratory and residential birds, because of the benefits of breeding with the same mate, but I think it will be a more important factor in migratory birds.

Black turnstones, *Arenaria melanocephala,* have a very high breeding territory fidelity: 88% in males and 87% in females. In this species, there is a high association between the high breeding site fidelity and a high mate fidelity. For black turnstones, the breeding site fidelity provides a mechanism for pair-mates to reunite. They are migratory and do not winter together. They also do not arrive at the same time after the winter, so pair formation generally occurs on the breeding territory itself. Mate fidelity is not just a consequence of nest site fidelity, because there are also pairs that reunite on new territories. The reunited pairs of black turnstones have a higher fledging success than new-formed pairs (Handel & Gill, 2000).

In piping plovers, *Charadrius melodus*, migratory birds, nest destruction and re-nesting is very common. Also, a lack of suitable, stable habitat increases the nest site fidelity. Remaining on the same territory, with the same mate, increases re-nesting speed. The birds are familiar with the surroundings and the mate, which increases their reproductive success. Their mate fidelity is usually high, intra-year mate switching is not common, but the fidelity fluctuates after nest destruction. If the nest is destroyed by a storm, not only their nest is destroyed, but a lot of nests are. This gives easy access to new mates (Haig & Oring, 1988).

The Sabine's Gull, *Xema sabini,* a migratory bird, shows very high site and mate fidelity. It breeds at high latitudes, where the breeding season is short. High site fidelity could reduce the time that is needed to search for a previous partner and thus promote early breeding. It could also enhance reproductive success, because the cooperation and coordination in parental activities could be increased. Most gull pairs breed within 100 meters of their previous nesting site, regardless of previous breeding success. The gulls have a strong fidelity to their mates, with the overall annual mate retention being 65% (80-88% in the first year, 63-75% in the second year and 20-33% in the third year). However, when a previous mate does not return, or returns late, the remaining mate quickly remates and stays with this new partner, even if the previous one returns later or in later years. (Stenhouse & Robertson, 2005)

Willow ptarmigans, *Lagopus logopus,* migratory birds, have a high site and mate fidelity. About 70% of the individuals whose partner returns to the site, actually pairs up with that partner. The pairs who have been together before have an earlier date of first egg than new pairs. This resulted in larger clutches, more chicks hatching and more chicks fledging. Female willow ptarmigans switch territories to get a better quality male, not a better quality territory. They also switch territory if the partner does not return to the area (Schieck & Hannon, 1989).

In hooded warblers, *Setophaga citrina*, also a migratory species, the divorce rate is high (57%). However, when a male defends the same territory as last year, the chance of his previous partner reuniting with him is higher, compared to males that defend a new territory. Female hooded warblers return to their previous territory more often when they pair up with the previous partner, compared to when they do not re-mate (or the partner does not return). The combination of familiar territory and mate is more attractive to a female, than only familiar territory or only familiar mate. When the population density is high, the competition between females increases the costs of searching for a former partner or competing for a former territory. This could be enough to outweigh the benefits, and thus decrease mate fidelity and site fidelity. (Howlett & Stutchbury, 2003)

In the kittiwake, *Rissa tradactyla*, a migratory bird species, most birds that stay together as a pair, also stay at the same site. When they separate and change partners, usually through divorce rather than death, one third of the males and two thirds of the females change sites as well (Greenwood, 1980). 92% of the females and 80% of the males that use the same nest site as the previous years retain their mates (tab. 5). This could indicate that the kittiwakes use the site fidelity to retrieve their previous mate (Fairweather & Coulson, 1995).

Another study shows they do not necessarily need the site to retain their previous mate. When forced to move, 73% of the females and 60% of the males that started breeding on another location retain their mates of the previous breeding season. Even of pairs that move to another colony 42% of the females and 30% of the males retain their mates of the previous breeding season. Not only when forced to move, they stay together, but also a lot of pairs stay together while moving site. 73% of the females and 60% of the males that changes nest sites divorces. (Fairweather & Coulson, 1995)

	Same window					
	Adjacent nest		Different ledge		Adjacent window	
	N	%	*N*	%	*N*	%
Male						
Same mate	13	54	9	35	23	44
Total*	24	100	26	100	52	100
Female						
Same mate	13	43	9	31	23	30
Total*	30	100	29	100	77	100

	>1 window		1 floor		>1 floor		Different side		
	N	%	*N*	%	*N*	%	*N*	%	Total *N*
Male									
Same mate	11	32	31	35	7	44	6	55	100
Total*	34	100	89	100	16	100	11	100	252
Female									
Same mate	11	21	31	24	7	23	6	33	100
Total*	53	100	131	100	31	100	18	100	369

Tab. 5. Movements within the warehouse colony by adult male and female kittiwakes that changed nest sites and could retain their mates (Fairweather & Coulson, 1995)

This means they use the site fidelity to retain mates, but it is not the only way to do so. They recognize each other as individuals and it is possible they move together.

The most frequent move is to a floor above or below the previous nest (they breed on the window ledges of buildings): 36% in females and 35% in males (tab. 6). Of the birds that changed nest sites and could retain their mate, 5% of the females and 4% of the males moved to a different side of the building. (Fairweather & Coulson, 1995)

	Site faithful		Change site	
	N	%	*N*	%
Male				
Same mate	835	80·0	100	39·7
Divorce	209	20·0	152	60·3
Total	1044	100	252	100
Female				
Same mate	835	92·4	100	27·1
Divorce	69	7·6	269	72·9
Total	904	100	369	100

Tab. 6. Pair status of male and female kittiwakes at the warehouse colony, in relation to nest site fidelity (Fairweather & Coulson, 1995)

Shortly after egg laying, the goldeneye male, *Bucephala clangula*, a migratory species, deserts his female. He also does not select or defend a nest site. Females do have a high site fidelity, but because of the minimal role of the male, this is more likely to be a result of locality, rather than mate.
Females that return to the same nest box can start laying earlier in the season, which gives them the opportunity to have a larger brood and a higher hatching success than females that do change nest boxes. (Dow & Fredga, 1983; Greenwood & Harvey, 1982)

42% of the goldeneye females reoccupies the same nest box in successive years. Females who did move, were less likely to hatch a successful brood than females that returned to their previous nest box. Their clutches and broods are smaller and they started breeding later in the season. 24% of the females that move, move to a first or second nearest-neighbour nest box and 80% of the total moving females moves to a nest box within the same cluster group of boxes as the old box. This gives a median of 0.75 kilometres from the old to the new nest box, which is about 10 nest boxes away (fig. 9) (Dow & Fredga, 1983). This is an example of relatively high nest site fidelity, without any male interference, since the goldeneye male plays no role in selecting or defending the nest site (Dow & Fredga, 1983).

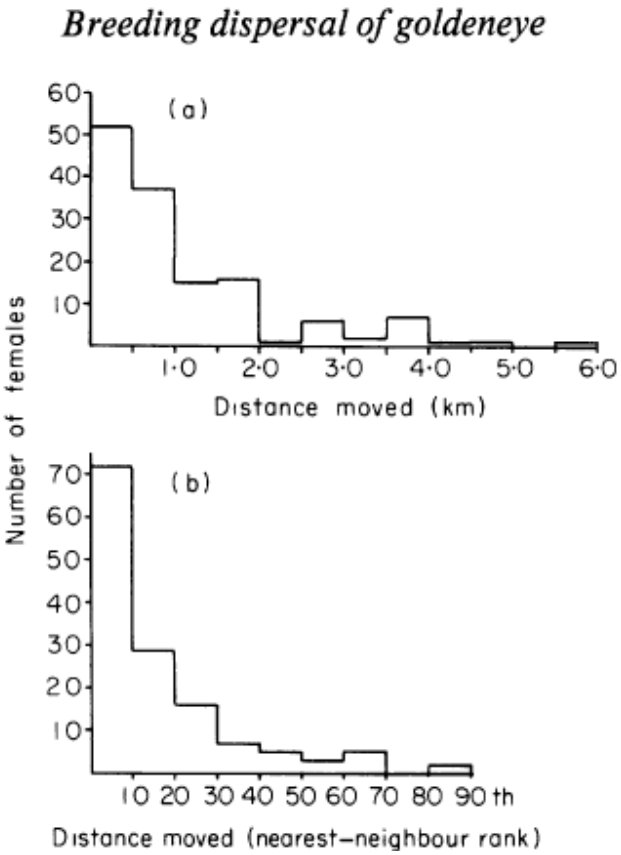

Fig. 9. Frequency distributions of the distances (a) and the nearest-neighbour ranks (b) that females moved from the old nest box to the new one (Dow & Fredga, 1983)

Great tits, *Parus major*, who are resident birds, have a high mate and site fidelity. Both sexes are very nest site faithful. After a divorce (29% of the birds who have the possibility of re-mating, do not), 80% of the males breeds within the same territory (fig. 10). Of the females however, only 40% breeds in the same territory. Only about 15% of the birds return to their previous nest box if they have a new mate. (Harvey *et al. 1979;* Greenwood, 1980). The median distance moved is between 50 meters and 143 meters (Harvey *et al*. 1979). This could indicate that in males the mate does not really influence the territory fidelity, or other factors might be of more importance, while in females the mate is a very important factor.

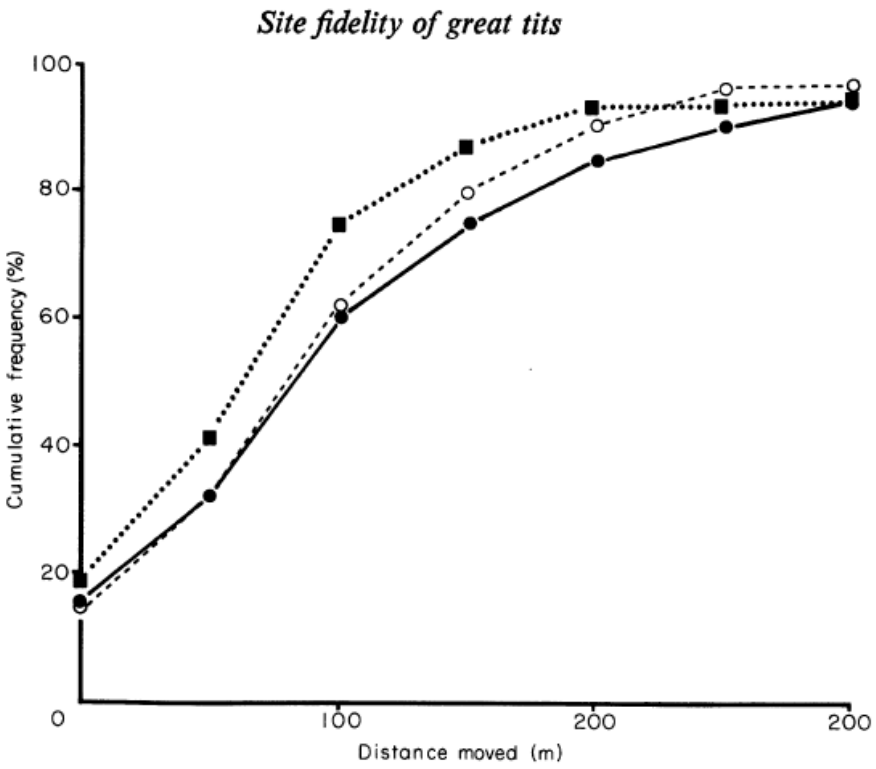

Fig. 10. Cumulative frequency plotted against breeding dispersal distance for maleswhose mates were presumed dead (O), for females whose mates were presumed dead (●) and for pairs nesting together in successive years (▪).

In most of the example species mate-fidelity is relatively high and this has an important influence on site fidelity. However, not every species seems to be highly influenced. This is also depends on how involved a mate is in the breeding process.

Discussion

A couple of general conclusions can be drawn. If a breeding attempt is successful, birds tend to stay close to the previous nest site. If a breeding attempt fails, it depends on the factor causing this failure, whether the birds stay or disperse away from the previous nest site (Newton & Marquiss, 1982; Dow & Fredga, 1983; Newton, 1985; Beletsky & Orians, 1987; Korpimaki 1987). Which factors are important for a bird depends on the species. Migratory birds disperse in general more than residential birds (Paradis *et al.* 1998).

But these conclusions are very general. I can not draw any conclusions on which factor is more important to birds and to which type of bird (migratory or residential) a certain factor is more important. In every factor I've looked at, I found examples for both migratory and residential bird species for which the factor influences their fidelity and examples for both migratory and residential bird species for which it does not. Field studies are usually focused on one or two species resulting in difficulties in identifying general ecological or evolutionary constraint (Paradis *et al.* 1998).

Because factors are looked at separately by a lot of studies, I cannot conclude which factors are most important to species when choosing to stay or move. Most likely is the scenario where every factor has some influence, one more than the other, and all costs and benefits added make a bird decide to move or not. Predation seems to be one of the key factors (e.g. Porneluzi, 2003). This is also one of the easiest factors to look at while studying a population. If a nest gets predated and a pair moves away, while pairs who do not get predated do not move away, this indicates a clear correlation. Too much rain could be more difficult to research, because this is an indirect factor and it is difficult to distinguish whether it is an important factor in the nest failure and/or decision to move away. When a female bird selects the same male and territory it had selected in previous years, it is difficult to distinguish whether the male itself, or the quality of the territory is the most important factor in the decision (Howlett & Stutchbury, 2003). And if she changes because of the quality of territory, does it mean there is not enough food? Or maybe the vegetation is not optimal. But one can also think of other environmental factors, which are not looked at in great detail yet. An example of this is microbial communities. It could be that the local microbes make a bird or its chicks sick, which could mean a lower reproductive success. If this is true, it could be an important factor in nest site fidelity.

In many articles they talk about a “successful” and “unsuccessful” breeding attempt (e.g. Haas, 1998). This does not give an idea on the “why”. Which factors have been an influence on this failure? Environmental factors? Or maybe infertility of one of the parents? Was there a lack of food? Was the weather bad? Was the nest predated? Predation is thought to be the primary cause of reproductive failure (Porneluzi, 2003), but one can not assume this is the case in every nest that fails.

Also, one can not say that if a factor is of influence in a couple of species, this means that all species of this type of bird are influenced by this factor. Predation for example, is important in some migratory species, like the ovenbirds, *Seiurus aurocapillus* (Porneluzi, 2003), the pied flycatcher, *Ficedula hypoleuca* (Haartmann, 1979) and the reed warbler, *Acrocephalus scirpaceus* (Catchpole, 1972), but does not seem to influence the dispersal in other migratory species, like the piping plover, *Charadrius melodus* (Haig & Oring, 1988) and the willow ptarmigan, *Lagopus lagopus* (Schieck & Hannon, 1989). Does this mean that the dispersal of migratory species in general is or is not influenced by predation? Between studies on the same species, not always the same population is used, which could also make a difference. This makes it difficult to

distinguish differences between migratory and residential birds.

One can think of more factors that could have an influence on the dispersal of a bird. Weather and the predictability of the weather are also factors in several species, like the piping plovers, *Charadrius melodus,* a migratory species (Haig & Oring, 1988). If the weather is very dry, or very wet, this can have consequences for the vegetation and the availability of food. So indirectly, weather conditions can have an influence on the success of a brood. This can be a factor in breeding dispersal. In some studies it is proven that the weather is a factor in dispersal, like how unpredictable rainfall in arid areas is a factor for the honey eaters (both migratory and residential), *Meliphagidae,* and the pink-eared duck in Australia, *Malacorrhyncus membranaceus,* which is a migratory bird (Greenwood & Harvey, 1982). They both tend to become nomadic if there is a lot of unpredictable rain (Greenwood & Harvey, 1982). During a study on black-billed magpies, *Pica pica,* a resident bird species, a snowstorm in 1987 caused a lot of breeding attempts to fail. This did not cause a switch in nest site, nor territory. (Dhindsa & Boag, 1992). But there are not many studies on this factor, which could be explained by its complex influence. It is difficult to link nest failure to a weather feature.

Furthermore, not only environmental factors influence dispersal, also non-environmental factors like age could determine whether a bird decides to stay or move (Pärt & Gustafsson, 1989; Alatalo *et al.* 1984). Also, some birds re-use their nests, like some birds of prey (Newton, 1979), colonial seabirds such as Gannets *Sula bassana* (Nelson, 1987) and Fulmars *Fulmarus glacialis* (Ollason & Dunnet, 1978). Others, build a new nest for every breeding attempt, like the stonechat (Greig-Smith, 1982) which automatically causes dispersal.

All in all I conclude that dispersal depends on a combination of environmental en non-environmental factors and it depends on the species and the circumstances which factors are more important. I think to get more detail on these processes research should be broader. Not look at one factor but examine more factors influencing one species, one population. If the same type of research is done on several species, one could draw better conclusions on general patterns, like comparing migratory and residential species. Also, because all the examples in this thesis are correlative studies, other factors can play a role, while experimental studies would make it possible to draw more conclusions on causality.

References

Alatalo, R. V., Gustafsson, L., Lundberg, A. 1984. Why have young passerine birds shorter wings than older birds? Ibis 126: 410-415.

Austin, O. L. 1949. Site tenacity, a behaviour trait of the common tern. Bird-Banding 20: 1-39

Bayne, E. M., Hobson, K.A. 2001. Movement patterns of adult male Ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. Condor 103: 343–351.

Beletsky, L. D., Orians, G. H. 1987. Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. Behavioural Ecology and Sociology 20: 21-34.

Berndt, R., Sternberg, H. 1969. Altersund Geschlechtsunterschiede in der Dispersion des Trauerschnappers *(Ficedula hypoleuca)*. J. Ornithol. 110: 22-26

Bibby, C. J. 1979. Foods of the Dartford Warbler *Sylvia undata* on southern English heathland (Aves:Sylviidae). J. Zool., Lond. 188: 557-576.

Blockstein, D. E. 1986. Reproductive behavior and parental investment of Mourning Doves *(Zenaida macroura)*. Ph.D. dissertation, Minneapolis, Univ. Minnesota.

Bollinger, E. K., Gavin, T.A. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk 106: 584–594.

Brooke, M. de L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater, *Puffinus puffinus*. J. Anim. Ecol. 47: 477-495.

Brooke, M. de L. 1979. Differences in the quality of territories held by wheatears (*Oenanthe oenanthe)*. J. Anim. Ecol 48: 21-32

Bulmer, M. G. 1973. Inbreeding in the great tit. Heredity 30: 313-25

Catchpole, C. K. 1972. A comparative study of territory in the reed warbler *(Acrocephalus scirpaceus)* and sedge warbler *(A. schoenobaenus).* Jr. Zool., Lond., 166: 213-231.

Chabrzyk, G., Coulson, J. C. 1976. Survival and recruitment in the herring gull *Larus argentatus*. J. Anim. Ecol. 45: 187-203

Coulson, J. C., Thomas, C. S. 1983. Mate choice in the Kittiwake Gull. Mate choice (P. Bateson, Ed.). London, Cambridge Univ. Press.: 361-376

Darley, J. A., Scott, D. M., Taylor, N. K. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. Bird-Banding 48: 145- 151.

Dhindsa, M., Boag, D. 1991. Patterns of nest site, territory, and mate switching in black-billed magpies *(Pica pica)*. Canadian Journal of Zoology, 70(4): 633-640.

Dhondt, A. A., Huble, J. 1968. fledging date and sex in relation to dispersal in young tits. Bird Study 15: 127-34

Dow, H. 1982. Breeding ecology of the goldeneye *Bucephala clangula*. PhD thesis. Univ. Newcastle, U.K.

Dow, H., Fredga, S. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. Journal of Animal Ecology, 52: 681-695.

Drilling, N. E., Thompson, C.F. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). Auk 105: 480–491.

Eagles, M. B. R. 1977. A study of the ecology of the Stonechat on Chailey Common, Sussex.- Unpublished report, 71 pp.

Eliason, B. C. 1986. Female site fidelity and polygyny in the Blackpoll Warbler *(Dendroica striata)*. Auk 103: 782-790.

Faaborg, J., Arendt, W. J. 1995. Survival rates of Puerto Rican birds: are islands really that different? Auk 112: 503–507.

Fairweather, J. A., Coulson, J. C. 1995. Mate retention in the kittiwake, Rissa tridactyla, and the significance of nest site tenacity. Animal Behaviour 50: 455–464.

Fisher, H. I. 1971. Experiments on homing in Laysan albatrosses, *Diomedea immutabilis*. Condor 73: 389-400

Galushin, V. M. 1974. Synchronous fluctuations in populations of some raptors and their prey. Ibis 116: 127-134

Gibb, J. A. and Betts, M. M. 1963. Food and food supply of nestling tits (*Paridae*) in Breckland pine. - J. Anim. Ecol. 32: 489-533

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140-1162.

Greenwood, P. J., Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annual Reviews of Ecology and Systematics 13: 1–21

Greenwood, P. J., Harvey, P. H., Perrins, C. M. 1979. The role of dispersal in the great tit *(Parus major)*: the causes consequences and heritability of natal dispersal. J. Anim. Ecol 48: 123-42

Greig-Smith, P. W. 1982. Dispersal between nest-sites by stonechats *(Saxicola torquata)* in relation to previous breeding success. Ornis Scandinavica 13: 232-238

Gustafsson, L. 1987. Interspecific competition lowers fitness in the collared flycatchers *Ficedula albicollis*: an experimental demonstration. Ecology 68: 291-296.

Haartmann, L. 1979. Der Trauerfliegenschnapper 1. Ortstreue und Rassenbildung. Acta Zool Fenn. 56: 1-104

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115: 929–936.

Haig, S. M. & Oring, L. W. 1987. Population studies of Piping Plovers at Lake of the Woods, Minnesota, 1982-1987. Loon 59: 113-117.

Haig, S. M. & Oring, L. W. 1988. Mate, site, and territory fidelity in Piping Plovers. Auk 105: 268–277.

Handel, C. M., Gill, R. E. 2000. Mate fidelity and breeding site tenacity in a monogamous sandpiper, the black turnstone. Animal Behaviour 60: 471- 481

Hannon, S. J., Martin K., Schieck J. O. 1988. Timing of reproduction in two populations of willow ptarmigan in northern Canada. Auk 105: 330-338

Harvey, P. H., Greenwood, P. J., Perrins, C. M. 1979. Breeding area fidelity of the great tit *(Parus major)*. J. Anim. Ecol. 48: 305-13

Harvey, P. H., Greenwood, P. J., Perrins, C. M., Martin, A. 1979. Breeding success of Great Tits in relation to age of male and female parent. Ibis 121: 186-200.

Hilden, O. 1979. Territoriality and site tenacity of Temminck's stint *Calidris temminckii*. Ornis Fenn. 56: 56-74

Holmes, R. T. 1971. Density, habitat, and the mating system of the Western Sandpiper *(Calidris mauri)*. Oecologia 7: 191-208.

Howlett, J. S., Stutchbury, B. J. 2003. Determinants of between-season site, territory, and mate fidelity in Hooded Warblers (*Wilsonia citrina*). Auk 120: 457-465.

Ingold, D. J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied woodpeckers and European Starlings. Auk 106: 209-217.

Ingold, D. J. 1991. Nest-site fidelity in Red-headed and Red-bellied woodpeckers. Wilson Bull. 103: 118-122.

Ingold, D. J. 1996. Between-year nest-site fidelity in Eastern Bluebirds in Ohio. Sialia 18: 43-47.

Korpimaki, E. 1987. Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. Journal of Animal Ecology 56: 185-196.

Lack, D. 1954. The Natural Regulation of animal numbers. Oxford: Clarendon

Lawn, M. R. 1982. Pairing systems and site tenacity of the willow warbler *Phylloscopus trochilus* in southern England. Ornis Scandinavica 13: 193-199.

Maher, W. J. 1979. Nestling diets of prairie passerine birds at Matador, Saskatchewan, Canada.- Ibis 121: 437-452.

Martin, S. G. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. Am. Zool. 14: 109-119.

Mills, J. A. 1973. The influence of age and pair-bond on the breeding biology of the red-billed gull, *Larus novaehollandiae scopulinus*. J. Anim. Ecol. 42: 147-63

Nelson, J. B. 1978. The Gannet. - Poyser, Berkhamsted.

Newton, I. 1972. Finches. London: Collins

Newton, I. 1979. Population Ecology of Raptors. - Poyser, Berkhamsted

Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. Journal of Animal Ecology 54: 241- 253.

Newton, I., Marquiss, M. 1982. Fidelity to breeding area and mate in the sparrowhawk *Accipiter nisus.* J Appl. Ecol. 51: 327–341.

Nice, M. M. 1937. Studies in the life history of the song sparrow. Part 1. Trans. Linn. Soc. NY 4: 1-247

Nice, M. M. 1943. Studies in the life history of the song sparrow. Part 2. Trans. Linn. Soc. NY 6: 1-328

Ollason, J. C., Dunnet, G. M. 1978. Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis,* in Orkney. - J. Anim. Ecol. 47: 961-976.

Oring, L. W., Lank, D. B. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyan-drous Spotted Sandpiper. Behav. Ecol. Sociobiol. 10: 185-191.

Oring, L. W., Lank, D. B., Maxson, S. J. 1983. Population studies of the polyandrous Spotted Sandpiper. Auk 100: 272-285.

Paradis, E., Baillie, S. R., Sutherland, W. J., Gregory, R. D. 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67:518–536.

Pärt, T., Gustafsson, L. 1989. Breeding dispersal in the collared flycatcher *(Ficedula albicollis)*: possible causes and reproductive consequences. J. Anim. Ecol. 58: 305-320.

Pinkowski, B. C. 1977. Breeding adaptations in the Eastern Bluebird. Condor 79: 289-302.

Porneluzi, P. A. 2003. Prior breeding success affects return rates of territorial male Ovenbirds. Condor 105: 73–79.

Porneluzi, P. A., Faaborg, J. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. Conservation Biology 13: 1151– 1162.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit *(Parus major L.)*. - J. Anim. Ecol. 39: 619-668.

Rohwer, S. 1983. Selection for adoption versus in-fanticide by replacement "mates" in birds. Current ornithology, vol.3 (R. F. John-ston, Ed.): 353-395

Rowley, I. 1983. Re-mating in birds. Mate choice (P. Bateson, Ed.). London, Cam-bridge Univ. Press. 331-360

Schieck, J. O., Hannon, S. J. 1989. Breeding site fidelity in Willow Ptarmigan: the influence of previous reproductive success and familiarity with partner and territory. Oecologia 81: 465-472.

Soikkeli, M. 1967. Breeding cycle and population dynamics of the Dunlin (*Calidrisa lpina*). Ann. Zool. Fennica 47: 158-198.

Stenhouse, I. J., Robertson, G. J. 2005. Philopatry, site tenacity, mate fidelity and adult survival in Sabine's Gulls. Condor 107: 416-423

Svardson, G. 1957. The 'invasion' type of bird migration. Brit. Birds 50: 314-43

Thorup, O. 1999. Breeding dispersal and site-fidelity in dunlin *(Calidris alpina)* at Tipperne, Denmark. Dansk Orn Foren Tidsskr 93: 255-265.

Vander Wall, S. B., Hoffman, S. W., Potts, W. K. 1981. Emigration behavior of Clark's nutcracker. Condor 83: 162-70

Vermeer, K. 1963. The breeding ecology of the glaucous-winged gull *(Larus glaucescens)* on Mandarte Island, B. C. Occ. Pap. Brit. Col. Prav. Mus. 13: 1-90

Weatherhead, P. J., Boak, K. A. 1986. Site infidelity in Song Sparrows. Anim. Behav. 34: 1299- 1310.

Wiens, T. P. 1986. Nest-site tenacity and mate re-tention in the Piping Plover *(Charadriusm elodus)*. M.S. thesis, Duluth, Univ. Minnesota.

Wooller, R. D., Coulson, J. C. 1977. Factors affecting the age of first breeding of the kittiwake, *Rissa tridactyla*. Ibis 1 19: 339-49

Wright, S. 1940. Breeding structure of populations in relation to speciation. Am. Nat. 74: 232-48

Wright, S. 1943. Isolation by distance. Genetics 28: 14-38

Wright, S. 1946. Isolation by distance under diverse systems of mating. Genetics 31: 39-59

Wunderle, J. M., JR. 1984. Mate switching and a seasonal increase in polygyny in the Bananaquit. Behaviour 88: 123-144.