The effect of interspecific competition on habitat selection in migratory birds: when to choose what?

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Migratory birds tend to have a selected amount of time to choose a suitable habitat. Therefore, they should make a quick decision in which the benefits and the costs of their habitat have been taken into consideration, whereby they gain as much fitness as possible. There are many factors that determine the quality of a habitat. The presence of resident species can give information about habitat quality, which is beneficial, but will also induce interspecific competition and interactions that bring fitness costs. The benefits of residents will outweigh the costs in a habitat with an intermediate density of residents. Therefore, migratory birds may maximize their fitness when selecting such a habitat.

Source image on front page: The four most common flight routes of most European birds.
http://www.noorderkempen.be/vogels/tekst/vogeltrek.htm

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Introduction

One of the most important decisions in the life of a bird is to select the right breeding habitat, because choosing a certain habitat largely affects its fitness. Since habitat quality can vary in factors that influence reproductive success, such as predator abundance, competitors and food availability, habitat selection is important for reproductive success. For example, it will be easier for an animal breeding in a habitat with sufficient food to raise healthy young than for an animal that breeds in scarcity.

Several factors influence breeding habitat quality in birds. First of all, nest site availability plays an important role: if there is no suitable place to build a nest, the habitat will be unsuited as a breeding habitat. Food availability is also a key factor in habitat quality. High food abundance means that more young can be raised with the same parental investment. Additionally, the quality of a habitat can be influenced by the presence of parasites and predators.
Furthermore, human activity can change the landscape, which in turn can influence factors like food and nest availability. However, even when birds find a habitat of high quality, some of them will be unable to breed in that habitat, because intrinsic factors like aggression, experience and quality of the bird may cause them to be unable to cope with the competition (Duckworth and Badyaev 2007, Duckworth 2006, Hakkarainen and Korpimaki 1996).

Habitat selection is most easily observed in migratory birds, since they choose a habitat quickly after arrival at their breeding grounds. Especially short-lived species cannot rely on past-experience and therefore their choice must depend on direct or indirect traits of the habitat. Therefore, in my thesis I will focus on the breeding habitat selection of migratory birds.

The presence of a competitor may be an important factors in habitat selection, as birds have been observed to be attracted to competitors. For example, in an experiment of Forsman et al (2002) 25 out of 36 male and 23 out of 25 female Pied flycatchers *(Ficedula hypoleuca)* chose a nest box near a breeding tit, indicating that Pied flycatchers were attracted to the vicinity of breeding titmice, suggesting that tit habitats were higher quality habitats. This is an example of migratory species using resident species as a cue for habitat quality.

The possible reason why migrants settle near residents is that they differ in information content about habitat quality. Resident birds live near their breeding habitat throughout the year, in contrast to migratory birds, who migrate to their breeding habitat in spring. In this way, residents have more time to collect information about habitat quality that helps them in deciding where they want to breed. Residents thus are expected to measure habitat quality directly, and make their choices based on habitat traits and competitor density. In contrast, migratory birds, who arrive shortly before their breeding onset and do not have a lot of time to invest in breeding habitat selection, may use the settling of residents with overlapping resource needs as an information source for habitat quality (Forsman et al 2002).

Besides that migrants benefit from using resident birds as information source for habitat selection, they may encounter costs due to the presence of those residents. As a result of the information use, migrants live in the proximity of residents with overlapping resource needs. Migrants and residents will therefore compete for those resources. This interspecific competition can lead to direct interspecific interactions that often result in injuries, which in turn can result in death. The abundance of resident species thus brings costs due to interspecific interactions.

Migrants have to choose a breeding habitat that has the highest possible reproductive success with the lowest costs of competition from competitors. Breeding in the proximity of residents can reduce the time invested in habitat selection, which is beneficial, because the saved time and energy can be invested in reproduction. Also, the habitats that house residents are probably of higher quality and breeding in a high quality habitat is beneficial for reproduction. On the other hand, migratory birds will encounter costs of interspecific competition when breeding in the proximity of resident heterospecifics. In order to gain maximal fitness by reproducing successfully, migrants have to choose a habitat in which the benefits outweigh the costs.

To get a better understanding of the selection forces of migratory birds in habitat selection with respect to interspecific interactions, I will review studies that have been done on these subjects. In these studies, various experiments concerning habitat selection and/or information use of residents are done. Sometimes, when habitat selection and the fitness consequences of that choice are tested, it is hard to conclude what really happened. For example, when migrants have to choose between a breeding habitat without residents and a breeding habitat with residents and the result of the study shows that the migrants in the latter have a higher breeding success, did the high fitness result from the breeding habitat or were only the birds with high fitness able to breed in that habitat? Here, I will critically overview earlier research and try to draw honest conclusions with respect to the actual results.

First, I will illustrate several factors that determine habitat quality, followed by an explanation of factors that influence habitat selection. Secondly, I will shortly discuss competition between birds. Then, I will discuss positive and negative effects of the proximity of competitors. Finally, I will discuss what the influence of interspecific competition on habitat selection is.

Habitat quality

A great variety of habitats can be found in nature. These habitats can differ in their suitability as a breeding area for birds, since some habitats create a great opportunity to raise young in, other habitats do not. The abundance of resident birds may reflect habitat quality, because residents have all year to judge the quality of habitats. In contrast, migrants arrive in their breeding areas shortly before breeding. In order to start breeding in time, it may be a better choice for a migrant to use residents as a cue for habitat quality, instead of estimating the quality of every potential breeding habitat themselves. The information that migrants use from residents are about several factors that influence habitat quality. In this

section I will discuss various factors, like the sort of nest place, predation risk, food availability and the presence of parasites.

The sort of nest place can be of importance for breeding habitat quality.
Loukola et al (2014) showed that pied flycatchers had a clear preference for nest boxes with substrate (fresh or old tit or flycatcher nest; sawdust) over empty nest boxes. They also found that pied flycatchers preferred nest boxes with sawdust over empty nest boxes and nest boxes with a fresh tit nest or fresh flycatcher nest in it. They found no fitness consequences (expressed in tarsus length and clutch size) between different boxes (Loukola et al 2014), but only 24 flycatchers chose boxes with a tit nest or flycatcher nest (2 in fresh and 10 in old tit nest, 2 in fresh and 10 in old flycatcher nest). Therefore, this study used a small sample size, which makes the conclusion questionable. The finding that nests built in empty nest boxes were heavier than those built on top of present substrate suggests that already available substrate may decrease the needed nest building effort.

Habitat quality can be affected by predation risk. This can be shown by the abundance of birds in a certain habitat. For example, Suhonen et al (1994) showed that the number of migratory birds, the number of species and the density of small birds increased as predation risk decreased along transects away from kestrel (predator) nests. Habitats further away were thus more suitable for small and migratory birds and therefore resulted in a higher habitat quality for these birds. Another example is that the suitability of Tengmalm's owl (*Aegolius funereus*)breeding habitats was decreased by the predatory interactions between Tengmalm's owls and its predators, Ural owls (*Strix uralensis*) and Eagle owls (*Bubo bubo*). Thereby, the population of breeding Tengmalm's owls was lower in the proximity of Ural and Eagle owls, resulting in a mean annual breeding occupation of 9% of all nest boxes close to and 25% of all nest boxes far away from the predating owls, measured over a timespan of sixteen years (Hakkarainen and Korpimaki 1996)

Predation risk is not only affecting the amount of birds in a habitat, but may also affect the fitness of the birds that are present. Morosinotto et al (2012) showed that Pied flycatchers had a smaller clutch size when the predation risk was higher. They suggested that the reduction in clutch size could be an adjustment in reproductive investment because of the high predation risk.

Food is one of the most important factors affecting reproductive success in birds. When there is not enough food around, there is less food available for the young, which can result in starvation, increased mortality among the young and eventually lead to reduced reproductive success. It is crucial for birds to choose a habitat that can provide enough food for their young. The amount of food in an area can therefore influence habitat quality.

There are many benefits to breeding in an area with a higher food availability. Hogstedt (1981) gave Eurasian magpie (*Pica pica*) pairs extra food before and during the breeding season. He compared the reproductive success with control groups that did not get extra food. The experimental pairs started to lay their eggs earlier, had larger clutch sizes, heavier eggs and a greater hatching success. A higher food abundance increased reproductive success. Dunn and Hannon 1992) illustrated a similar result when they looked at the effects

of food abundance and male parental care on reproductive success in Tree swallows (*Tachycineta bicolor*). They compared two areas that differed in food abundance and found that the area with a higher food availability gave rise to polygyny, which allowed secondary females to lay more eggs and produce more fledglings than females in the other area, that were coupled to monogamous males.

Another factor that contributes to habitat quality is the presence or absence of parasites and pathogens. They can have an enormous impact on the fitness of a bird, by causing disease symptoms which could lead to the death of the host (Lindström, 2000).

Habitat quality could depend on the infestation of these harmful micro-organisms. A habitat with a lower abundance of parasites would be preferred. For example, Loye and Carroll (1998) found that American cliff swallows (*Hirundo pyrrhonota*), long distance migrants, did not return to colony sites that were infested with parasites, but they did reoccupy the portion of the site that had been sprayed with a DDT insecticide. The cliff swallows seemed to be able to make a difference in habitat quality regarding the high or low presence of parasites.

Parasite presence has been suggested to be the reason for some bird species to migrate to the north, since there is a reduced exposure to parasites (Piersma 1997). Figuerola (1999) found evidence that species living in more saline habitats had fewer haematozoic parasites (blood parasites) than freshwater birds. Thus, the amount of exposure to parasites and pathogens could play a role in migratory birds in determining the habitat quality and therefore selecting their habitat.

Another form of parasites is the brood parasite. Brood parasites are birds that do not build nests or raise young on their own. Instead, they lay eggs in a host bird's nest. The most famous example of a brood parasite is the cuckoo. The brown-headed cowbird is a brood parasite of up to 200 different bird species in North America, including migratory birds. A study by Forsman and Martin (2009) suggested that hosts use vocal cues of parasites to indicate the density of cowbirds and local risk in estimating habitat quality. Migratory birds selected their habitat after listening to the vocal cues avoided crowbird areas, while resident birds and non-host species decided beforehand and did not respond to the vocal cues.

There are also factors that play a role in habitat quality that are not directly reflected by the abundance of residents. Nest availability is one of those important factors in habitat quality. A habitat without suitable places for nest building cannot serve as breeding habitat. The amount of available nest places can affect habitat quality. Gustafsson (1988) found that the breeding densities of Collared flycatchers (*Ficedula albicollis*), Blue tits (*Parus caeruleus*) and Great tits (*Parus major*) increased with providing extra nest boxes, not taking the interspecific competition between these species into account. In Swedish Lapland, adding nest boxes to the area increased the bird density with 75% (Enemar en Sjöstrand, 1972). Merila and Wiggins (1995) showed that the number of Collared flycatcher casualties inside nest boxes decreased with increasing box number per hectare. Therefore, birds will experience less competition when more suitable nest places are present.

Other factors are human activity, infrastructure and landscape. For example, the presence of House sparrows (*Passer domesticus*) increased with increasing proportion of intensive cultures, buildings and livestock density (Robillard et al 2013). The suitability of a habitat, and therefore habitat quality, may therefore depend on the amount of the described human influences.

So far, I discussed different factors that influence habitat quality. I discussed them separately. However, in nature, there is always a combination of several factors that determines the quality of a certain habitat.

Habitat selection

The fact that a habitat is a potential good breeding habitat does not mean that all birds are going to breed in it. Not all individuals are able to obtain the preferred habitats. In this section, I will discuss factors that may contribute to habitat selection. Thus, what factors may cause a bird to choose a breeding habitat with certain properties and quality?

Habitat selection can be affected by aggression. Aggression plays an important role in the fierce competition for available nest sites, because it increases the ability to secure nest cavities (Duckworth 2006, Merila and Wiggins 1995). An example of this are Western bluebirds, in which the more aggressive males obtained the territories with multiple nest boxes, that were preferred. The more aggressive males were also the males that dispersed, while the less aggressive males stayed where they were raised (Duckworth and Badyaev 2007). These results suggest that aggression is an important factor in habitat selection.

Experience can have an effect on habitat selection. Unlike an experienced individual, an unexperienced bird has never bred before and therefore faces the stages of reproduction, including habitat selection, for the first time. Because of the gained experience, experienced individuals might have an advantage in habitat selection. As one might say: practice makes perfect.
Indeed, Hakkarainen and Korpimaki (1996) found that in Tengmalm's owls, the unexperienced males bred in habitats that were unfavorable in terms of high predation risk. They suggested that intraspecific competition drove unexperienced males into these habitats that had a higher predation risk. Thus, experienced Tengmalm's Owl males probably had a higher chance of getting a high quality habitat than did unexperienced males.

A study by Remacha and Delgado (2009) illustrated that infrastructure and landscape played an important role in habitat selection in three different bird species. They showed that nest boxes close to buildings and close to the forest edge were more likely to be occupied by House sparrows, while boxes further away were mostly occupied by Great tits and Tree sparrows (*Passer montanus*). This suggests that there was species-specific habitat selection, induced by the infrastructure of the area. Thus, infrastructure and landscape can play a role in breeding habitat selection.

Habitat selection can be affected by the presence and abundance of competitors. This is seen in different bird species. For example in Tengmalm's owls, where short-winged females were probably driven to mate with males in suboptimal habitats, because long-winged females would be superior in intra-sexual competition (Hakkarainen and Korpimaki 1996). Robillard et al (2013) showed that the density of sparrows reduced the nest box occupancy of swallows. Another example is found in flycatchers, who compete with tits for nest sites and food. Forsman et al (2002) showed that Pied flycatchers preferred habitats with breeding tits over habitats without tits and suggested that the Pied flycatchers were attracted to their vicinity. The number of casualties in another flycatcher species, the Collared flycatcher, increased with proportional occupation by tits (Merila and Wiggins 1995). This result suggests that Collared flycatchers should select another habitat when a lot of tits are present and therefore that the abundance of competitors affects habitat selection.

Competition between birds

Different birds may be in need of the same resources. This means that those birds face competition when they breed in proximity of each other. Birds of the same species do of course need the same sort of food and nest sites, but different species can also have the same need for resources.

For example, Pied flycatchers and tits compete for food. The Pied flycatcher takes a greater variety of prey than the great tit, but there is dietary overlap in food items that they feed their young with (Slagsvold, 1975). The Great tit's and Pied flycatcher's diet mainly exists of caterpillars and arachnidas, although the Pied flycatcher eats diptera and coleoptera as well ((ROYAMA 1970, Sanz 1998). Török (1986) compared food overlap between the migratory Collared flycatchers *(Ficedula albicollis)*, Great tits and Blue tits. Tits and flycatchers had a considerable niche overlap in the breeding season: the overlap between Great tits and Collared flycatchers in Hungary was 33% and between Blue tits and Collared flycatchers 45%. These results prove that interspecific competition for food can take place between migratory and resident bird species.

Food is not the only thing that birds can compete for. They also experience competition for nest sites. When studying competition for nest sites between the Great tit and Pied flycatcher, Tompa (1967) found that in plots with a low density of nest boxes, where nearly all were occupied, almost every pair of tits experienced heavy competition from flycatchers. Schmidt (1957) found 130 nest boxes occupied by tits in early spring, but later in spring, after the arrival of Pied flycatchers, 16 of those boxes (12%) were occupied by Pied flycatchers, suggesting that nest box take-overs and therefore competition for nest sites take place in these species.

Positive effects of the proximity of competitors

Often is thought that competition is something that affects fitness negatively, but breeding close to competitors may bring benefits. In this section, I will discuss possible benefits of the proximity of interspecific and intraspecific competitors.

As discussed above, migrants may use residents as a source of information about habitat quality (Forsman et al 2002). This may for example happen in Pied flycatchers, who used

Great tits for habitat selection (Seppänen and Forsman 2007). The abundance of resident Great tits can indicate that a habitat is of high quality. Great tits are present near their breeding area all year, which means that they have enough time to determine the quality of different habitats and can choose a suitable one to breed in. The resource needs of Great tits overlap with those of the Pied flycatcher, thus Great tit abundance shows that needed resources are available in that habitat. This suggests that habitats where Great tits are present are of higher quality than habitats without Great tits. More generally, habitats where residents are present are of higher quality for ecologically alike migratory species and thus, migrants can use residents as a cue for habitat quality.

Forsman et al (2002) showed that Pied flycatchers that bred in areas with tits started laying eggs earlier after arrival than flycatchers in areas without tits. Also, the eggs hatched earlier and the mean brood size was higher, resulting in 0.6 more flycatcher nestlings in tit areas than in non-tit areas. Nestlings that were born in nest boxes next to a tit's nest box were heavier and had longer wings. Forsman et al (2007) found a positive effect of Great tit presence on tarsus and wing length in nestlings of Pied flycatchers. These results showed that the breeding success of migrants was higher in proximity of resident birds and may indicate that habitats in which residents are present are indeed of higher quality than habitats without residents.

Additional to the use of information about habitat quality, migratory birds can use residents to reduce nest building effort. Loukola et al (2014)showed that Pied flycatchers used less nest material for their nest if they built their nest on top of an existing nest or substrate compared to nests built in empty nest boxes. Doing this saves energy, which means that more energy can be invested in reproduction. However, there were no differences in fitness (expressed in tarsus length and clutch size) found between boxes with substrate and empty boxes. But since predation risk is relatively high during nest building (Dale and Slagsvold 1996), a reduced period of nest building can increase the survival chances of the female Pied flycatcher. Therefore, using the nest of a resident may enhance fitness.

Intraspecific competitors may also have a positive effect on fitness. Conspecific attraction is the tendency for individuals of the same species to settle near each other (Ward & Schlossberg, 2004). For example, colonial birds prefer to breed near conspecifics. It can be beneficial to stay close to conspecifics because they might serve as cues for habitat quality and groups are more effective at territory defense, predator protection, or attracting prospective mates (Muller et al 1997).

Negative effects of the proximity of competitors

So far, I discussed positive effects of the proximity of competition, but there are also negative effects. Here, I will discuss negative effects that birds may experience when breeding in the proximity of their competitors.

Intraspecific competition may lead to fitness costs. Conspecifics are in need of the same resources. This means that they may compete when they breed in proximity of each other. It also means that they may compete for breeding habitat. A result of competition for breeding habitat is that the superior individuals of a population will be able to occupy a

breeding spot in high quality habitats, while subordinate individuals are forced to settle in low quality habitats. Breeding habitat largely affects fitness, so breeding in a habitat of low quality may bring serious fitness costs.
An example that shows lower fitness in low quality habitats was found by Hakkarainen and Korpimaki (1996) in Tengmalm's owls. They found a reduced breeding frequency and delayed onset of egg laying in individuals that bred in high predation risk habitats, compared to individuals breeding in low predation risk habitats. They suggested that the males competed for habitats and the females for mating options, what resulted in a distribution of the assumed superior experienced males and long-winged females in habitats with low predation risk and assumed subordinate short-winged females and young males in habitats with high predation risk. In this research, unfortunately, it remains unclear whether the lower fitness is really an effect of habitat quality or that it can be ascribed to bird quality. However, Morosinotto et al (2012) found that Pied flycatchers in high predation risk habitats had smaller clutch sizes than Pied flycatchers of similar quality in low predation risk habitats. This supports the idea that intraspecific competition for resources can have a negative effect on the fitness of birds.

Not only the presence of intraspecific competitors, but also that of interspecific competitors may lead to fitness costs. Above, I discussed that migratory birds can be attracted to the vicinity of resident species, because the presence of ecologically similar residents may reflect a high habitat quality. This is only possible if the resident and migratory species are in need of the same resources. Te presence of migratory and resident birds that need the same resources leads to interspecific competition. This competition can be very fierce, as often is seen in different flycatcher species that compete with resident tit species for nest sites and food. For example, 23 Collared flycatchers were found dead inside (mostly Great) tit nest boxes during the breeding season of 1993 (Merila and Wiggins 1995). This was 4.2% of the breeding population of all study plots, but was up to 17% in a given plot. The effect may have been even bigger, since some deaths could have been missed.

Ahola et al (2007) described that 53 dead Pied flycatchers were found in South-Western Finland from 1953-2005. It could be that only low quality birds died this way, but probably also higher quality birds are likely to pay the costs of this competition, since (Great) tits are physically dominant (Ahola et al 2007) and flycatchers therefore barely have a chance to exit a nest box intact after an interaction with a tit. But, on the other hand, you might consider a bird that makes a poor decision (entering a tit's nest box at the wrong time) a low quality bird.
The Collared flycatchers and Pied flycatchers of the discussed studies were all killed due to interactions with the Great tit or Blue tit in the competition for nest sites. Interspecific competition therefore played a role in adult mortality in Collared and Pied flycatchers. This effect will be stronger when tit density is high, because interspecific interactions will increase (Forsman et al 2007).
Interspecific competition thus may lead to serious injury and death, which terminates the reproductive success of participants, leading to a huge loss in fitness.

Conclusion

There are several factors that can influence the quality of a habitat, like the sort of nest place, predation risk, food availability and the presence of parasites. This causes a great variety of habitats with different qualities to be found in nature. Some habitats are of high quality and are suitable for breeding and some habitats have a low quality and do not offer great opportunities for breeding.

The results of Loukola et al (2014) showed that Pied flycatchers avoided nest take-overs when a similar kind of nest material (sawdust) was available. This was probably to avoid costs of competition. This means that when migrants can choose between a nest option that is likely to result in competition and a nest option that does not, they choose for the one without competition risk. This makes sense, because competition can bring fitness costs.

However, migrants preferred habitats with residents (Forsman et al 2002) and thus with interspecific competition. This was probably because the quality of habitats that include resident birds are higher than habitats without them. There is also evidence that some migrant species have a higher breeding success when breeding in the proximity of residents (Forsman et al 2002, Forsman et al 2007).

Since habitat selection experiments and fitness measurements are combined in the studies that have been done, it is unclear whether the higher breeding success is the result of habitat quality or that only high quality birds selected habitats with residents. Namely, breeding near competitors leads to competition, which is not without risks and can lead to fitness costs (Merila and Wiggins 1995, Ahola et al 2007). Maybe only high quality birds are able to cope with this competition.

This competition is fierce and could lead to death. The migrants that were found dead were flycatchers killed by tits inside a nest box. Since tits are physically dominant over flycatchers, I think that no matter what the quality of the flycatcher is, it is likely to be killed by a tit when it enters a tit's nest box at the wrong moment. Flycatchers are more skilled in terms of flying, so when the interaction takes place outside a nest box, the flycatcher will be in advantage. So, I think that a low quality flycatcher can still escape a tit when outside a nest box, suggesting that the costs for interspecific competition are not caused by the quality of the flycatcher. Therefore, I think that the higher breeding success is caused by the quality of the habitat.

So, when do migrants have to choose for a certain habitat? There are several factors that influence habitat selection, like experience, aggression, infrastructure, landscape and the abundance of competitors. To be able to gain fitness, it is important to make sure that benefits outweigh costs. Because migrants need to take various factors into account when selecting a breeding habitat and those factors all have their own costs and benefits, it is difficult to know the overall costs and benefits of a certain habitat. Migrants want to select a habitat with the highest quality and the lowest cost, so they can maximize fitness. They have to select a habitat in which resources are sufficient but on the other hand in which they can handle the interspecific competition.

A habitat of high quality probably houses a lot of residents, which would induce a lot of (harmful) interspecific interactions if a migrant settles in that habitat. I think that the costs of the interspecific competition in this habitat outweighs the benefits. A habitat in which the benefits outweigh the costs of interspecific competition, thus intermediate densities of residents, probably is the best choice for a migrant. Forsman et al (2008) already showed that in Collared flycatchers there is an optimal trade-off between competition and facilitation when the density of Great and Blue tits was intermediate.

Habitat selection can differ between birds. The situation in a habitat is different for a late arriving migrant than for a migrant that arrived early. The early arriving migrants are first to select a breeding habitat and may therefore occupy high quality habitats. This means that when late arriving migrants arrive in the breeding area, the quality of those habitats may be changed due to the presence of their conspecifics. The early arriving migrants selected the habitat because it would be beneficial for them, but when migrants keep selecting that habitat, it might eventually not be beneficial anymore, because breeding density will deplete resources, and it would be better to select another habitat that at first was considered of lower quality.

To conclude, selecting a habitat is a dynamic process that depends on a lot of internal and external factors, including the presence of interspecific competitors and the competition they bring. Every migrant has already invested a lot of energy in reproduction when they migrated to the breeding grounds. Therefore, it is of high importance that, once they arrived, they make the best possible decision when selecting a habitat, so their investment pays of in terms of fitness.

In the future, more research can be done in order to be more certain of what caused the higher breeding success in migrants when they bred in the proximity of residents. For example, an experiment where heterospecific information is manipulated or an experiment in which birds are forced to breed in a certain habitat or at certain nest sites may give insight in the use of social information in habitat selection with respect to fitness consequences. Until then, it is difficult to truly understand the effect that residents have on habitat selection of migratory birds.

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