

# Nest box reuse in a migrating bird is independent of nest content

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Site fidelity after successful nesting is an adaptation to spatially heterogeneous and temporally auto-correlated risk of nest predation. Cavity-nesting common goldeneye (*Bucephala clangula*) females use this strategy to minimize nest predation from pine marten (*Martes martes*), but because goldeneyes migrate they may save time when deciding where to nest by relying on information about successful nests gained in the previous year. I tested whether reuse of a nest box where the previous nest was successful is affected by the content. After a goldeneye had successfully nested, I manipulated nest box availability by offering two nest boxes; one in the original nest tree and one in a new tree for the season, each containing either old nest material from the successful nest or new nest material, i.e. wood shavings. The boxes were installed and relocated when goldeneyes were absent from the study area. The manipulation was designed to test whether goldeneyes reuse a cavity based on information conveyed by its current content, or on private or public information gained in the previous nesting season. Goldeneyes consistently reused the box in the original nest tree, independent of box content. Thus, when the information available in the current nesting season conflicted with information acquired in the previous nesting season, the goldeneyes relied on the latter rather than on information that would cost valuable time to update after arrival in spring. The common practice among ornithologists and land managers to clean nest boxes after each nesting would not affect cavity reuse in the goldeneye.



## 1. Introduction

In birds, the use of private information to decide on site fidelity after successful nesting is a well-known adaptation to spatially heterogeneous and temporally auto-correlated predation risk (e.g. Dow & Fredga 1983, 1985, Schmidt *et al.* 2006; Chalfoun & Martin 2010, Chalfoun & Schmidt 2012). In addition, breeding outcome often produces public information, available by

prospecting nest sites of conspecifics, and even of heterospecifics, in the current breeding season (Chalfoun & Schmidt 2012). Targeting successful nest sites next year for successful reproduction depends on spatially heterogeneous and temporally auto-correlated predation risk, which is a prerequisite for both informed fidelity and informed dispersal (Doligez *et al.* 1999, Pöysä 1999, 2006, Schmidt 2004, Schmidt *et al.* 2010).

Common goldeneyes (*Bucephala clangula*),

hereafter termed goldeneyes, are medium-sized diving ducks (female body mass c. 700 g) that nest in tree cavities over large parts of the Holarctic boreal forest (Cramp & Simmons 1977). They migrate and are absent from most of the breeding grounds during winter, except when or where lakes or rivers remain ice-free throughout the year (Cramp & Simmons 1977). In the western Palearctic goldeneyes nest mostly in cavities excavated by the black woodpecker (*Dryocopus martius*), but readily use nest boxes (e.g. Dow & Fredga 1983), which makes experimental studies feasible (e.g. Pöysä *et al.* 2001). The ducklings leave the nest within two days after hatching, and the female does not return to the nest thereafter (Cramp & Simmons 1977, Pöysä 2006). Hence, after having been successfully used for nesting by goldeneye, the nest cavity contains eggshell membranes and fragments of the hatched eggs as well as the down that the female has plucked and used for covering the eggs during incubation and recesses (Eadie & Gauthier 1985, Pöysä *et al.* 2014), hereafter termed old nest material. The presence of this material may be used as a cue of a safe nest site (Pöysä 2006, Pöysä *et al.* 2014).

Goldeneyes in the western Palearctic are exposed to a significant risk of nest predation by the pine marten (*Martes martes*) (Dow & Fredga 1983, 1985, Johnsson *et al.* 1993a, Pöysä *et al.* 1997), which is a medium-sized (c. 1 kg) tree-climbing mustelid with relatively large home range (on average 7 km<sup>2</sup> at 60°N in Sweden and Norway) and a generalist diet (Brainerd 1997, Helldin 1999). The risk of predation by pine marten on nests of the goldeneye was higher in boxes where the previous nest was depredated than in boxes where the previous nest was successful (Dow & Fredga 1985, Pöysä 1999, 2006). One explanation of this pattern may be that pine marten remembers the location of cavities it has found, and revisits them each nesting season (Sonerud 1985a, 1989, 1993, ElMBERG & Pöysä 2011). Another not mutually exclusive explanation is the site effect, where some nest sites are simply more exposed to predators than are others (Martin *et al.* 2000). Indeed, goldeneyes have been found to shift nest box use more often after nest predation than after a successful nesting (Dow & Fredga 1983). Failed breeders, potential brood parasites and 1-year old females prospect for nest sites, both

when conspecifics are incubating as well as later in summer, and the following year they use boxes where the nesting was successful in the previous year (Eadie & Gauthier 1985, Zicus & Hennes 1989, Pöysä *et al.* 1999, Pöysä 2006). Even females that have nested successfully have been observed prospecting the same summer (Zicus & Hennes 1989). Thus, when assessing predation risk goldeneyes seem to use the presence of material from successful nesting as a cue (Dow & Fredga 1985, Pöysä 1999, 2006), and seem unable to assess the relative predation risk of previously unoccupied boxes (Pöysä *et al.* 2001).

While goldeneye females shifted to another nest box the next year in 89% of the cases when they had their nest depredated, they shifted to another nest box the next year in no less than 45% of the cases when they had nested successfully (Dow & Fredga 1983). However, Dow and Fredga (1983) could not identify the cues on which the females based their decision to reuse the same nest box or shift to another one after successfully nesting. Dow and Fredga (1983) routinely cleaned out all boxes at the end of each breeding season and relined them with wood chips. Therefore, the goldeneye females would have faced conflicting information on the content of the same nest box in the current and the previous year, and the individual females may have differed in their relative use of information from the current season and the previous season (cf. Schmidt *et al.* 2010). It is possible that some of the goldeneyes studied by Dow & Fredga (1983) based their nest site selection on current information conveyed by box content rather than on private or public information gained in the previous nesting season, and thus avoided the cleaned boxes because they were not able to separate them from previously unoccupied boxes.

To test whether goldeneye reuse of a cavity where the previous nest attempt was successful is affected by the current cavity content, I carried out a field experiment. At each locality where a goldeneye female had nested successfully the previous year, I provided goldeneyes a choice between two boxes. The experiment consisted of three treatments manipulating the box content to test whether the reuse of a nest cavity by female goldeneyes is affected by information conveyed by its current content, and not only

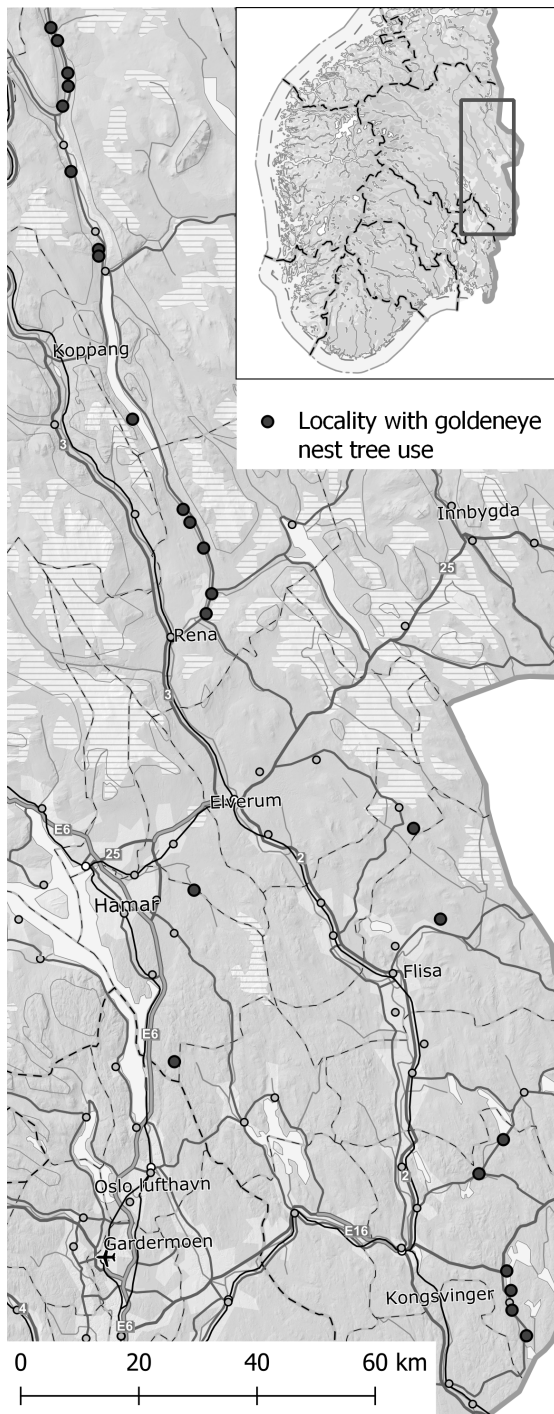


Fig. 1. Map of southeast Norway showing the extent of the study area and the positions of the 24 localities where the 51 analysed cases of goldeneye nest tree use occurred.

on the cavity's spatial position as learned in the previous nesting season from private or public information on its content of old nest material. By presenting boxes in a dyad at each nesting locality I was able to separate the choice of nest cavity from the choice of breeding locality. The design of the experiment produced conflicting information for the birds while selecting a nest site (Schmidt *et al.* 2010), allowing me to assess the importance of nest material as a cue for safe nest sites. This would contribute to our understanding of nest site selection behaviour of cavity nesting species and also to the management of those species using artificial nest boxes.

## 2. Materials and methods

### 2.1. Study area

The study was conducted during 1988–1998 at altitudes ranging 160–580 m a.s.l. within 60°03'–62°04'N and 11°03'–12°22'E in Hedmark county (from 2020 part of Innlandet county) in southeastern Norway (Fig. 1). The study area is situated in the boreal zone and consists mostly of coniferous forest (Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)) that is managed for commercial harvesting and activities include unselective clear-cutting, regeneration by planting, and thinning by selective cutting. In Hedmark county there is ca. 21 000 lakes, which together cover 1 268 km<sup>2</sup>, i.e. 4.6% of the county's area of 27 388 km<sup>2</sup>.

### 2.2. Nest boxes

Nest boxes made of wooden board and lined with a 5–10 cm deep layer of fine wood shavings covering the bottom were installed 5 m above ground. They were accessed using ladders, and inspected by removing the roof. The boxes had an inner bottom area of ca. 20 cm × 20 cm, a depth of ca. 30 cm, and a circular entrance hole with a diameter of ca. 10 cm. In comparison, natural cavities excavated by the black woodpecker in Norway and

Sweden were on average 7 m above ground, and had a depth of 31 cm and an entrance 8 cm wide and 11 cm high (Johnsson *et al.* 1993b, Rolstad *et al.* 2000). The boxes were installed in single trees in clear-cut areas if possible, or in trees on edges between clear-cuts and old forest, independent of distance to lakes and rivers. This reflected the habitat preferences of black woodpeckers selecting a tree in which to excavate a nesting cavity (see Rolstad *et al.* 2000), and made the boxes attractive for goldeneyes as well (cf. Pöysä *et al.* 1999).

The boxes were visited 1–6 times (95% CI 2.5, 2.7) between late March and early July each year to record nesting attempts by goldeneyes, and to ring the female. Female goldeneyes were trapped by hand or by use of a landing net when incubating, and were released at the nest site immediately after ringing.

### 2.3. Experimental treatment procedure

The term locality denotes one box until the first successful nest by a goldeneye, and a dyad of boxes in the years thereafter. I performed all experimental manipulation between September and April. This is well after the period when goldeneye females prospect for a cavity to target for egg laying next year (Eadie & Gauthier 1985, Zicus & Hennes 1989, Pöysä 2006). Successful females do not visit their own nest after the brood has left it (Pöysä 2006). Hence, when they returned in spring the goldeneye females in my study were faced with a different nest box set-up than the one they had experienced the previous summer.

In treatment 1, the box in which goldeneye had nested successfully (in year  $t$ ) was relocated with its contents of old nest material to a new tree, and a box lined with new wood shavings was installed in its place (Fig. 2) If the goldeneye did not use any of the two boxes for nesting in the following season (year  $t+1$ ), the original box was relocated once more to a further new tree, and the wood shavings in the box on the original nest tree was renewed. In this way, when arriving in spring the goldeneye females had the choice between the box with the old nest material in a new tree for the season, and a box lined with new wood shavings in the original tree (Fig. 2). The

information conveyed by the content of the boxes in the current nesting season was thus opposite to and in conflict with the information in a natural situation, where new cavities without old nest material appear at new sites as a supplement to old ones with old nest material still present.

In treatment 2, the box in which goldeneye had nested successfully (in year  $t$ ) was left in place with its original content of old nest material, and a new one was installed in another tree (Fig. 2). If the goldeneye did not use any of the two boxes for nesting in the following season (year  $t+1$ ), the new box was relocated once more to a further new tree, and its content of wood shavings renewed. In this way, when arriving in spring the goldeneye females had the choice between a box lined with new wood shavings in a new tree for the season, and the box with the old nest material in the original tree (Fig. 2). The information conveyed by the content of the boxes in the current nesting season was thus the same as in a natural situation.

In treatment 3, the box in which goldeneye had nested successfully (in year  $t$ ) was exchanged with a new one, and another new box was installed in another tree (Fig. 2) If the goldeneye did not use any of the two boxes for nesting in the following season (year  $t+1$ ), the new box in the new tree was relocated once more to a further new tree, and the wood shavings in both boxes renewed. In this way, when arriving in spring the goldeneye females had the choice between a box lined with new wood shavings in a new tree for the season, and a box lined with new shavings in the original tree (Fig. 2). The information conveyed by the content of the boxes in the current nesting season was thus in conflict with the information in a natural situation, and provided no cues to the goldeneyes for choice of nest site.

I conducted three treatments at each locality if possible. In all treatments, I installed the spatially new box in the same species of tree as the original nest tree and in a habitat as similar as possible, and made sure that this box could not be seen from its previous position or from the box in the original tree. These constraints defined the distance between the two boxes, which ranged 50–440 m when box choice occurred. The two boxes in a dyad had identical shape and size. Also, they were worn to a similar degree, because boxes were stored outdoor when not being used in the study.

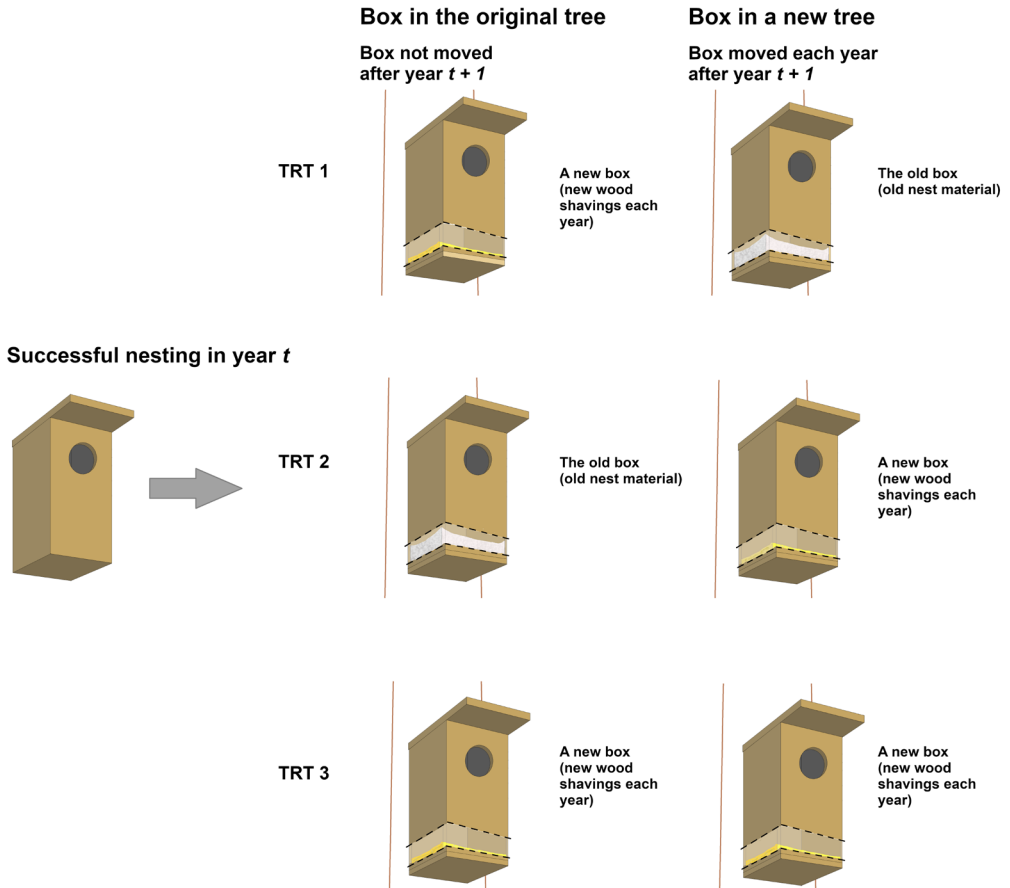


Fig. 2. The experimental procedure following a successful nest consisted of three treatments (TRT) to provide the goldeneyes with two options each nesting season; a box containing new wood shavings in the original nest tree vs. a box containing the old nest material from the successful nest in a new tree for the season (TRT 1); a box containing the old nest material from the successful nest in the original nest tree vs. a box containing new wood shaving in a new tree for the season (TRT2); and a box containing new wood shavings in both the original nest tree and a new tree for the season (TRT 3).

Therefore, they differed only in their spatial position and content.

I defined a box as being used when at least one goldeneye egg had been laid there (cf. Pöysä *et al.* 2001). If the nesting in this box was successful, the tree was used as the original nest tree in the next treatment at the locality. If the nest was depredated or deserted, the two boxes were left in place until a successful nesting took place in one of them. Then the experiment continued as described above. If all nesting attempts by goldeneye in this study had been successful, four nesting attempts at one locality would have been sufficient for all three

treatments to be performed. However, due to nest predation and nest desertion, at most locations more than  $N+1$  nesting attempts were needed in order to perform  $N$  treatments.

I regarded treatment 1 as the radical one, differing most from the natural pattern reflected in treatment 2, whereas I regarded treatment 3 as the control. Treatment 1 produced conflicting information for the goldeneyes (cf. Schmidt *et al.* 2010), while treatment 3 mimicked the situation where boxes are cleaned out after the breeding season (cf. Møller 1989, 1992). Therefore, at each locality, I usually conducted treatment 1 first

(mean rank  $\pm$  SE  $1.2 \pm 0.2$ ), thereafter treatment 2 (mean rank  $1.8 \pm 0.2$ ), and finally treatment 3 (mean rank  $2.3 \pm 0.2$ ). Increasing rank in the order of treatments would reflect a longer presence of two boxes at a locality, but not a longer time elapsed since the successful nesting there.

## 2.4. Data analysis

I used one case in one treatment as unit in statistical tests. It might be argued that the pattern of nest site choice found would be biased by using each case in a treatment as population unit in statistical tests, because such an approach might violate the assumption of statistical independence, and inflate sample size. However, if the intra-individual variation can be demonstrated to be at least as large as the inter-individual variation, pooling observations will not bias the results or increase the probability of making a type I error (Leger & Didrichsons 1994). The 8 females known to be involved in two treatments and the 3 females known to be involved in three treatments reused the box in the original tree in all treatments, and it is unknown whether the only one exception to the observed selection pattern of reusing the box in the original tree was due to intra- or inter-individual variation (see Results). Hence, weighing the risk of pseudoreplication against reduction in sample size, I decided to also present data from all treatments in all cases.

Whether the goldeneyes used the box in the new tree rather than the box in the original tree was tested with one-tailed Binomial test (Siegel & Castellan 1988). Differences between the three treatments for how long a nest box had been present in the original tree, and for distance between the two boxes in the dyad, were tested with two-tailed one-way ANOVA in JMP<sup>®</sup> version 15 (SAS 2019). Estimates are given with  $\pm 1$  SE.

## 3. Results

### 3.1. Nest number and characteristics

The study was based on a total of 216 goldeneye nesting attempts, recorded at 80 localities, with 1–7 attempts per locality. Of these, 58 were

depredated or deserted, or had unknown fate, when only one box was present. Hence, a second box could be added as an experimental treatment in 79 cases. Of these, 28 failed to give data for analysis for various reasons. Among these were three cases when a goldeneye female had used one box and boreal owls (*Aegolius funereus*) had occupied the other box at the locality. There was doubt as to whether the goldeneye made its choice first, and thus whether both boxes were available when the goldeneye initiated breeding. Correspondingly, in four of the cases where goldeneye females occupied both boxes at a locality there was doubt about which box was occupied first and these cases were excluded. The number of cases used in the analysis was 19, 17 and 15 in treatments 1, 2 and 3, respectively. These 51 cases were from 24 different localities (Fig. 1).

The number of nesting seasons that a box had been present in the original nest tree at a locality when the goldeneye made its selection differed marginally non-significantly between rank in the order of treatments ( $F_{2,48} = 3.06$ ,  $p = 0.056$ ), and was on average  $4.8 \pm 0.3$ ,  $5.3 \pm 0.4$ , and  $6.2 \pm 0.5$  for rank 1, 2 and 3, respectively. The number of years elapsed since the original successful nesting at a locality, and the distance between the two boxes, did not differ significantly between rank in the order of treatment ( $F_{2,48} = 0.89$ ,  $p = 0.42$ ,  $F_{2,44} = 0.16$ ,  $p = 0.85$ , respectively).

In 48 of the 51 cases the original successful nesting had taken place the year before the goldeneye made its choice between the two experimental options. In the three remaining cases, the original successful nesting had taken place two years before. When the goldeneye made its choice of nest tree, a box had been present in the original nest tree for an average of  $5.2 \pm 0.2$  (range 2–8) nesting seasons, differing significantly between the three treatments ( $F_{2,48} = 6.38$ ,  $p = 0.0035$ ), being on average  $4.3 \pm 0.3$  ( $N = 19$ ),  $5.9 \pm 0.4$  ( $N = 17$ ) and  $5.7 \pm 0.4$  ( $N = 15$ ) in treatment 1, 2 and 3, respectively. The number of years elapsed since the original successful nesting at the locality was on average  $1.1 \pm 0.2$  (range 1–2) years, and did not differ significantly between the treatments ( $F_{2,48} = 1.34$ ,  $p = 0.27$ ). The distance between the two boxes was on average  $162 \pm 13$  m ( $N = 47$ , 4 cases not recorded), and did not differ significantly between the treatments ( $F_{2,44} = 0.58$ ,  $p = 0.56$ ).

### 3.2. Female identity

In 26 of the 51 cases included in the analysis, the breeding goldeneye female was trapped at both the pre-treatment nest (in year  $t$ ) and the treatment nest (in year  $t+1$ ). The case was scored as “same” if the same female was trapped at the pre-treatment nest and the treatment nest ( $N = 23$ ), and “new” if the identity of the female trapped at the pre-treatment nest was different from that of the female trapped at the treatment nest ( $N = 3$ ). In 18 of the 25 remaining cases the missing identification was due either to predation of the treatment nest before attempted trapping ( $N = 4$ ), or to unsuccessful or cancelled trapping at the pre-treatment nest ( $N = 10$ ) or the treatment nest ( $N = 4$ ). In these 18 cases, the female was scored as “unknown”. In the remaining seven cases, however, the female had either been trapped in the same (original) nest tree the year before the missing trapping at the pre-treatment nest ( $N = 4$ ), or the year after the missing trapping at the treatment nest ( $N = 3$ ). In all these cases the female turned out to be the same as the one nesting there two years after or two years before, respectively, suggesting that the same female nested there in the intermediate year as well. The female in these cases was therefore scored as “probably same”.

Among the 23 cases of females scored as “same”, 9 involved a female that was represented in one or two other treatments. Correspondingly, among the 7 cases of females scored as “probably same”, 3 involved a female that was represented in one or two other treatments. Finally, among the 3 cases of females scored as “new”, one involved a female that was involved in 2 cases as “same”. Thus, among these 33 cases, 20 different females were involved. Among the 18 cases of females scored as “unknown”, one would therefore expect 7 to involve females represented in more than one treatment, and 11 different females to be involved.

### 3.2. Choice of nest tree

In treatment 1, the goldeneye females used the original nest tree in all cases, and thus significantly preferred to nest in a new box in the original nest tree rather than in the original box with the old nest material in a new tree (Fig. 3, Binomial

test,  $p < 0.001$ ). In treatment 2, they used the original nest tree in 94% of the cases, and thus significantly preferred to nest in the original box with the old nest material in the original nest tree rather than in a new box in a new tree (Fig. 3, Binomial test,  $p < 0.001$ ). Finally, in treatment 3, when given the choice between nesting in a new box in the original nest tree and a new box in a new tree, they significantly preferred the former (Fig. 3, Binomial test,  $p < 0.001$ ), and used the original nest tree in all cases. Thus, with only one exception, the goldeneye females used the original nest tree independently of the content of the associated nest box, and therefore their spatial nest box selection pattern did not differ between the three treatments (Fig. 3). In the only exception to this pattern, the box that the female avoided contained old nest material (treatment 2) with fleas at the time of nest site selection.

Females scored as “same” reused the original nest tree, whether or not the box contained an original nest, in all treatments (Fig. 3), and this preference was significant (Binomial test,  $p = 0.001$ ,  $p = 0.03$  and  $p = 0.004$ , in treatments 1, 2 and 3, respectively). Also, females scored as “probably same” reused the nest box in the original nest tree in all treatments, which was a significant preference (Binomial test,  $p = 0.008$ ). Females scored as “new” showed numerically the same spatial nest box selection pattern as did females scored as “same”, but the sample was very small (Fig. 3) and precluded a statistical test. Females of unknown identity showed the same spatial nest box selection pattern as females scored as “same” (Fig. 3,  $\chi^2 = 1.31$ ,  $df = 1$ ,  $p = 0.25$ ).

Limiting the use of each identified female to only one case, reducing the sample size to 20 for “same”, “probably same”, and “new” pooled (see above), the nest box in the original nest tree was used in all cases, which was a significant preference (Binomial test,  $p < 0.001$ ).

## 4. Discussion

In the present experiment goldeneye females consistently used the original nest tree where the previous nest was successful, rather than the new tree, independent of which tree housed the box that contained the old nest material that conveyed

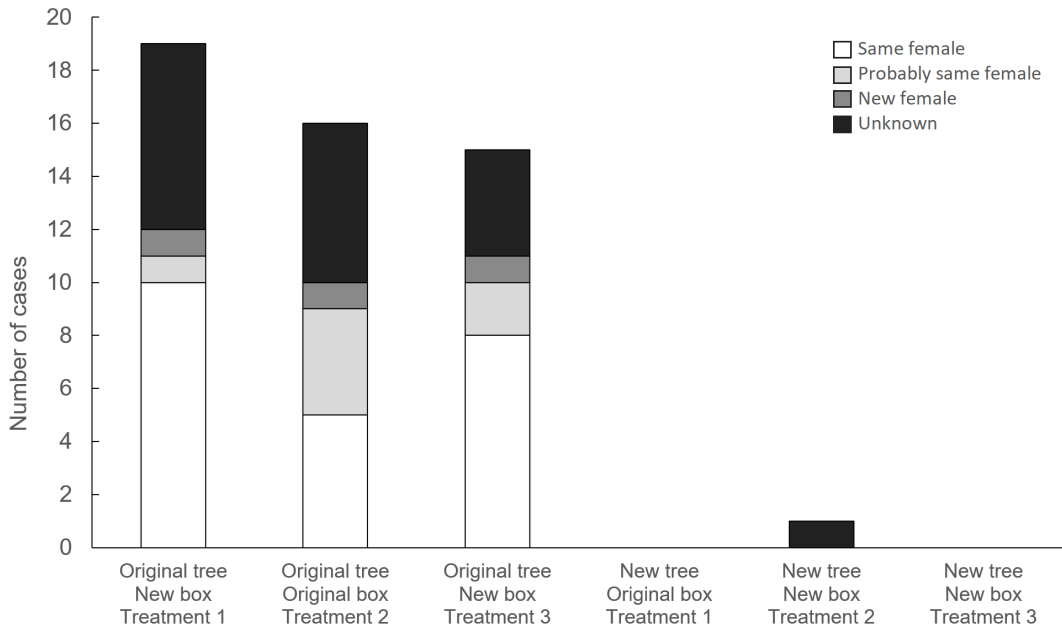


Fig. 3. The nest tree and the nest box used by goldeneye females in the three experimental treatments (treatment nest). In all cases a goldeneye female had nested successfully in the original box in the original tree, either 1 year ( $N = 48$ ) or 2 years ( $N = 3$ ) earlier (pre-treatment nest). White parts of the columns denote cases where the same female incubated the treatment nest and the pre-treatment nest. Light grey parts denote cases where probably the same female incubated the treatment nest and the pre-treatment nest. Dark grey parts denote cases where a new female incubated the treatment nest. Black parts denote cases where it was unknown whether the same or a new female incubated the treatment nest. See text for a detailed explanation of female identity.

information on the previous successful nesting. When faced with conflicting information, i. e. the new tree housing the box with the old nest material (treatment 1), the females never used this tree, but rather the original tree with the box lined with new wood shavings. This demonstrates unequivocally that the goldeneye females did not base their choice on information conveyed by the current box content.

No information conveyed by the content of the two boxes (treatment 3) is equivalent to a situation where the box with a successful nest last year is cleaned and relined with wood chips before the next nesting season, as in the study of Dow and Fredga (1983, 1984, 1985), and compared with a box with no previous nesting. Dow and Fredga (1983, 1985) found that goldeneye females had a higher nest site fidelity after a successful nest than after having their nest depredated and that they were more likely to occupy a box in which the nest in the previous year escaped predation than a

box in which the nest was depredated. Moreover, a box that had been unoccupied in the previous year was not more likely to be used than a box in which the nest was depredated in the previous year, but each of these options was less likely to be used than a box in which the nest was successful the previous year (Dow & Fredga 1985). Similarly, goldeneye females were more likely to lay eggs parasitically in a box where there was a successful nest the previous year than in a box where the nest was depredated the previous year and a box where there was no nest the previous year (Pöysä 1999). This fits the lower risk of depredation in boxes that escaped predation last year than in boxes that were empty last year and boxes where the nest was depredated last year (Dow & Fredga 1985, Pöysä 2006). However, when goldeneye females had to choose among previously unoccupied boxes, their choice was not correlated with the difference in risk of nest predation between these boxes, as measured by predation on artificial eggs (Pöysä *et al.* 2001).



Thus, without information on the outcome of previous nesting attempts, goldeneye females seem unable to choose among available nest boxes so as to minimize predation risk (Pöysä *et al.* 2001). This is supported by my results, which show that the information conveyed by the current content of the box did not affect the reuse of nest tree. This suggests that the goldeneye female remembers the spatial position of the tree where there was a successful nest last year, whether this was her own nest or the nest of a conspecific female, the latter located by prospecting (Eadie & Gauthier 1985, Zicus & Hennes 1989, Pöysä *et al.* 1999, 2001, Pöysä 2006). Pöysä (2006) found that the rate of prospecting in a nest box in one year predicted the probability of nest parasitism in the box the next year.

Goldeneye females are migratory in most of Fennoscandia (e.g. Cramp & Simmons 1977) and unable to search for cavities during a substantial part of the non-breeding season. Therefore, they are severely time-constrained in their search for cavities when they return in spring. In fact, goldeneye females who returned to the box that they used the previous year laid their eggs earlier than those that changed nest site (Dow & Fredga 1983, 1984), but were more exposed to nest parasitism from conspecifics (Dow & Fredga 1983, Pöysä 1999, 2006). My results demonstrate that goldeneye females, when faced with conflicting information, used the spatial information on successful nests gained in the previous year, regardless of what happened in that nest in the meantime, and did not use the information available after arrival in spring prior to breeding. Interestingly, there was no difference in nest site use between “same” and “new” goldeneye females in my experiment, but the sample of the latter was very limited. Because the migrating goldeneye female cannot update her information on the cavity feature outside the breeding season, her strategy is vulnerable to changes between nesting seasons, for instance that the cavity is found by the Pine Marten in winter and revisited in spring. The pine marten visits cavities year round and uses them for roosting, denning and food storing (Sonerud 1985b, Brainerd *et al.* 1995), and would take any suitable prey that may happen to be there, including eggs and nestlings. This predation is probably to a large extent learned (cf. Sonerud 1985a, 1989, 1993), because pine

martens spend most time on the ground and prey mainly on small mammals (Pulliainen & Ollimäki 1996, Helldin 2000).

Because the goldeneyes reused the box in the original nest tree in all cases except one, they might have been unable to find the box in the new tree. However, in several cases another goldeneye occupied the latter box (see Methods). Also, the boxes were installed in open habitats and were visible from a long distance (see Methods). In general, goldeneye females are very capable of finding new nest sites (Pöysä *et al.* 1999, 2014). Hence, I do not regard the strong preference for the box in the original nest tree to be caused by an inability to find the box in the new tree for the season. On the other hand, in the cases where the same female returned and found a box in the same position in the same tree as the box she successfully nested in the previous year she may have had little incentive to explore for nest sites elsewhere.

Reusing a cavity with material from a successful nest may carry the cost of increased level of microbial infection and ectoparasites, even in a precocial species like the wood duck (*Aix sponsa*) (Utsey & Hepp 1997, Walls *et al.* 2012). However, this cost must be traded against the lower risk of nest predation where the previous nest was successful (Mazgajski 2007). In altricial birds there seems to be no consistent negative effect on reproductive success of selecting cavities with old nest material (Mazgajski 2007), while a study on the wood duck suggests negative effect (Utsey & Hepp 1997).

Based on the fact that nest boxes deviate fundamentally from natural nest sites because they have been created by the researchers themselves, Møller (1989, 1992) questioned the validity of results from nest box studies in general, and the effect of enhanced cavity quality represented by nest boxes in particular, for instance the common practice of removing old nest material. In my experiment, removing old nest material did not affect the nest box reuse by female goldeneyes, and would therefore not bias any estimate of the natural breeding dispersal. This is fortunate for the interpretation of the results on nest site selection and dispersal presented by Dow and Fredga (1983, 1985), who cleaned out all boxes at the end of the season, and thus kept no control boxes with old nest material.

In conclusion, by manipulating the content of old nest material in spatially old and new boxes I was able to separate information acquired by goldeneye females in the previous nesting season from information available to them in the current one. When the goldeneye females were faced with this conflicting information, they clearly based their use of nest site on information already acquired in the previous nesting season rather than on information that would cost valuable time to update after arrival in spring.

### Telkänpönttöjen uudelleenasettaminen ei riipu pesämateriaalista

Onnistuneen pesinnän jälkeen linnut jäävät usein samalle pesimäpaikalle. Tätä pidetään usein sopeutumana alueellisesti ja ajallisesti vaihtelevaan saalistuspaineeseen. Telkkä on kolopesijä, joka käyttää tätä strategiaa vähentääkseen näädän aiheuttamia pesätuhoja. Koska telkät ovat muuttolintuja, ne saattavat nopeuttaa pesimäpaikan valintaa valitsemalla pesäpaikkoja, joissa pesintä oli aiempina vuosina onnistunut. Tutkimuksessa selvitettiin, riippuiko onnistuneen pesinnän pöntön uudelleenkäyttö siitä, että oliko pöntössä pesämateriaalia. Onnistuneiden pesintöiden jälkeen alueelle sijoitettiin kaksi pönttöä, joista toinen alkuperäiseen pesäpuuhun ja toinen uuteen. Pöntöissä oli joko vanhaa pesämateriaalia tai uutta materiaalia (puulastuja). Pöntöt sijoitettiin talven aikana, kun linnut eivät olleet pesimäalueella. Koeasetelmalla testattiin, käyttävätkö telkät informaatiota pesän nykyisestä statuksesta, vai tekevätkö ne valinnan edellisen vuoden kokemuksen perusteella. Havaittiin, että telkät valitsivat aiemmin käyttämänsä pesäpuun, riippumatta pesäpöntön sisällöstä (vanha/uusi pesämateriaali). Kun aiempi ja uusi tieto pesimämenestyksestä (pesän sisältö) olivat ristiriidassa, telkät perustivat valintansa aiemman vuoden tietoon, ja tällä tavalla säästivät aikaa uuden pesimäpaikan etsimiseltä. Tulosten perusteella pesäpönttöjen puhdistaminen ei vaikuta telkkien pesimäpaikan valintaan tai informaatioon.

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