The effect of nesting habitat on reproductive output of the Barn Swallow (*Hirundo rustica*). A comparative study of populations from atypical and typical nesting habitats in western Poland

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ABSTRACT. The aim of this study was to discover if atypical nesting places such as abandoned second world war bomb shelters and conditions occurring within, can constitute suitable and good quality alternative habitat for the Barn Swallow. To answer this question, the time of breeding, clutch size and the mean survival probability of nest contents were compared between swallows nesting in shelters and in farm outbuildings – typical nesting habitat. The study showed that bunkers do constitute a suitable and relatively good quality alternative habitat for the Barn Swallow but they are poorer nesting places than pigsties or cowsheds. Mean survival rate of nest contents (eggs/nestlings) was higher in farm outbuildings than in bunkers, but only differences in the first broods were recorded. The results are most probably the effect of different conditions occurring in the two kinds of nesting habitat, especially at the beginning of the breeding season, when the unfavourable weather conditions can negatively influence breeding swallows to a higher degree in bunkers than in outbuildings.

KEY WORDS: Barn Swallow, *Hirundo rustica*, reproduction, shelters, survival analysis

INTRODUCTION

The Barn Swallow *Hirundo rustica* is a farmland, long distance migratory, insectivorous passerine bird that has declined in some parts of its European breeding range during recent decades (Møller, 1989; Marchant et al., 1990; Tucker & Heath, 1994; Møller & Vansteenwegen, 1997; Ambrosini et al., 2002a; Papazoglou et al., 2004; Wretenberg et al., 2006). The main causes for decline in abundance in its breeding range are most probably intensive agricultural practices, disappearance of individual livestock farms, especially those raising cattle, and the removal and refurbishment of old farm buildings leading to a loss of nesting opportunities (Marchant et al., 1990; Weggler & Widmer, 2000; Møller, 2001; Ambrosini et al., 2002b; Evans et al., 2003; Robinson et al., 2003). By virtue of its large range and population size, the Barn Swallow is not a species of special concern (Papazoglou et al., 2004), but extremely high breeding philopatry (Saino et al., 2002) and social facilitation of breeding habitat choice may delay response of populations to rapidly changing ecological conditions in anthropogenic habitats (Ambrosini et al., 2002b). In the case of habitats with superabundant insects, where availability is not exactly related to grazing animals (eg. flooded river valleys), the removal and refurbishment of old farm buildings – typical nesting places, seems to be the most important factor responsible for distribution and abundance of the Barn Swallow. In such circumstances, the alternative nesting places create breeding opportunities and to some degree can compensate for changes in habitat and simultaneously increase the chances for the local populations to survive.

To date, studies on breeding biology and ecology of the Barn Swallow have been carried out in the most typical nest sites used by this species, such as inside derelict buildings, cowsheds, pigsties, stables and other similar outbuildings where animals are raised, as well as in different kinds of domestic buildings (Adams, 1957; Kuźniak, 1967; Löhrl & Gutscher, 1973; Møller, 1982; Turner, 1982; Bańbura & Zielński, 1998; Giacchini & Piangerelli, 2001; Møller, 2001). Furthermore, it is known that Barn Swallows nest in less specific, atypical places such as under roofs of different kinds of buildings, in rock crevices, under bridges, in mine shafts, wells, jetties and in culverts (Vietinghoff-Riesch, 1955; Weiner 1967; Davies & Tucker 1984; Tryjanowski & Lorek, 1992; Turner, 2006). However, in most cases there is a complete lack of data about the breeding biology or ecology from such nesting habitats. Other atypical breeding habitats of the Barn Swallow are abandoned second world war bomb shelters (Czechowski & Zduniak, 2005). Such places differ from the typical nesting habitats with regard to light and water conditions, temperature, predation pressure and direct access to food such as flying insects. They also, to some degree, resemble primeval nesting places of the Barn Swallow such as caves, grottos and rocky crevices (Turner, 2006).

The aim of this study was to investigate whether atypical places such as abandoned second world war bomb shelters and conditions occurring within, can constitute suitable and good quality alternative habitat for the Barn

Swallow. This is of interest especially in the context of areas with decreasing numbers of the Barn Swallow, where alternative, atypical nesting places can increase the chance for the local populations to survive. To answer the question, the main breeding parameters of swallows nesting in shelters were compared to populations occurring in typical nesting habitats.

MATERIAL AND METHODS

The breeding biology of the Barn Swallow has been studied by many researches in many places and at different times. These differences make it difficult to directly compare the results obtained from other studies. For example, there are differences in habitat or atmospheric conditions influencing food resources, which in turn affect many breeding parameters (e.g., KUŹNIAK, 1967; MØLLER, 1984; TURNER, 2006). Hence, the only solution to this kind of difficulty is to compare the breeding parameters of populations studied at the same time, located close to each other and in similar environmental conditions such as the same river valley. For this reason during the study of the Barn Swallows in bunkers, another nearby but typical nesting population of this species was studied using the same methods.

The fieldwork was carried out during four breeding seasons (from the end of April to the end of August) in 2004-2007 simultaneously in two areas in the Odra river valley, W. Poland, located 52km from each other. The first of the areas was situated near Czerwińsk (52°01'N, 15°26'E), where Barn Swallows nested in 13, abandoned second world war shelters built in 1939, being a part of the Odra war embankment (detailed description of bunkers in CZECHOWSKI & ZDUNIAK, 2005). The second area was Kłopot (52°7'N, 14°43'E) – a small village located 1km from the channel of the Odra river, where there are 50 small farms with a population of 200 inhabitants. In this area, swallows nest in the farm outbuildings. The number of farms and outbuildings visited varied during the study period from three to 10 and from nine to 22, respectively. On average in 89.1% (SE=1.21, range: 86.4-92.3; n=4) of the outbuildings animals were raised (mainly pigs, cows, rabbits, chickens) and 10.9 % (SE=1.21, range: 7.7-13.6; n=4) of the outbuildings were derelict.

In comparison to the outbuildings, the shelters were characterised by relatively low and stable air temperature and water occurring inside especially in the first stage of the breeding season. The shelters were on average 5ºC cooler than outbuildings (Wilcoxon matched-pairs test, Z=2.20, n=6, p=0.028; mean temperature values in ºC for the same 6 days and the same time during the breeding season; shelters: $\bar{x}$=13.5±0.34; outbuildings: $\bar{x}$=17.7±0.84).

The study sites were visited at intervals depending on the stage of broods and were shorter (4-5 days) during the most important events such as egg laying and nestling rearing periods and longer (8-9 days) during the incubation period and between the first and second broods. The mean number of visits per season in the four years of study was 14.0±1.87 (range: 10-19) in bunkers and 13.0±0.82 (11-15) in outbuildings. During each visit, all nests in individual shelters and outbuildings were checked and in every active nest the number of eggs, and later the number of nestlings was recorded. The mean number of first and second broods observed each year was 38.2±4.97 (range: 30-50) and 22.5±3.92 (17-34) in bunkers and 33.3±4.21 (23-43) and 21.3±1.43 (17-23) in outbuildings, respectively.

The reproductive parameters such as clutch size and the mean survival probability of nest contents expressing the reproductive output were compared between populations breeding in bunkers and typical nesting population of this species.

Data processing and analysis

The ages of eggs and nestlings were estimated on the basis of the date of laying of the first egg, established by direct observation or calculated assuming that one egg was laid per day (i.e. KUŹNIAK, 1967; TURNER, 2006). The age estimations of eggs and nestlings were supported by the use of the field instruction "Euring Swallow Project" from 2001 prepared by the Ornithological Station of the Museum and Institute of Polish Academy of Sciences.

Survival was calculated on the basis of changes in the number of eggs and nestlings in the nests observed and the life tables method was applied (KLEINBAUM, 1996). This method assumes that survival is a function of time, which enables the identification of the critical moments occurring during the reproduction period in the populations studied. The best element of the life tables showing the critical periods is hazard rate defined as the probability per time unit that an individual that has survived to the beginning of the respective interval will die in that interval. In general, the higher the hazard rate the higher the risk of failure and the same the lower survival, whereas the lower the values of hazard rate the higher the survival.

The survival time of each individual (egg/nestling) was estimated from the day when the egg was laid in the nest to the day of the last visit of each nest. The day when eggs or nestlings failed was calculated as half way between two subsequent nest visits (ZDUNIAK, 2010).

To compare survival between many groups, the multiple sample test was used, which is an extension of Gehan's generalized Wilcoxon test (GEHAN, 1965), Peto and Peto's generalized Wilcoxon test, and the log-rank test (PETO & PETO, 1972; LEE, 1980). Multiple comparisons between two groups were made using the Cox-Mantel test (COX, 1959; 1972; MANTEL, 1966) and the Bonferroni correction was applied.

Overall, the material was analysed using life tables including two cohorts of a total number of 1041 eggs from 222 clutches (376 eggs in 2004, 251 in 2005, 199 in 2006 and 215 in 2007) observed in bunkers and 953 eggs from 204 nests (289 eggs in 2004, 260 in 2005, 220 in 2006 and 184 in 2007) recorded in farm outbuildings. To check if the data from the four years of study can be pooled, the possible effect of a year on the survival was tested with the use of the Cox's proportional hazard model (COX, 1972). This model assumed that hazard rate is a function of independent variables. Use of this model allows the estimation of regression coefficients for independent variables. In general, variables with positive coefficients are associated with a higher risk of failure and decreased survival, whereas variables with negative coefficients are connected with a lower risk of death and increased survival (ZDUNIAK, 2010).

Besides the survival, differences at the time of breeding were also analysed (expressed as Julian days of the first egg laying in each nest) and clutch size between study areas using factorial ANOVA, where the year effect was also controlled. It was not possible to acquire the complete set of information for each nest, and thus sample sizes varied in analyses. The standard statistical methods used in this paper were described by SOKAL & ROHLF (1995). Throughout the text, all mean values are presented with standard errors (±SE). All calculations were performed using STATISTICA for Windows (STATSOFT INC, 2008).

RESULTS

Time of breeding and clutch size

The time of the first broods initiation did not differ between study areas (factorial ANOVA, $F_{1,245}$=2.85, p=0.09; bunkers: $\bar{x}$=51.5±1.3, n=134, outbuildings: $\bar{x}$=48.4±1.3, n=119). The same was found for the second broods ($F_{1,160}$=1.99, p=0.16, bunkers: $\bar{x}$=100.1±1.6, n=83, outbuildings: $\bar{x}$=97±1.5, n=85).

Mean clutch size in the first broods was higher than in second broods (factorial ANOVA, $F_{1.418}$=88.41, p<0.001) and was 4.98±0.05 (n=264) and 4.31±0.06 (n=170), respectively. Moreover, mean clutch size in both broods did not differ between study areas ($F_{1.418}$=0.94, p=0.33).

Survival of eggs and nestlings

The initial analysis with the use of the Cox's proportional hazard model, where year and study area were the factors, showed significant differences in survival between study areas and no effect of the year (whole model: chi-square =12.65, df=2, p<0.002; study area: ß = -0.16±0.04, Wald statistic =12.21, p<0.001; year: ß = -0.01±0.02, Wald statistic =0.20, p=0.65). For this reason the data from four years' study were pooled.

Mean survival rate of nest contents (eggs/nestlings) for the whole nesting period (40 days – from the egg laid to fledgling) for both study areas was 0.754±0.010 (n=1994), and was higher in outbuildings than in bunkers (Cox-Mantel test = -7.30, p<0.001). However, the recorded differences concerned first broods only (Cox-Mantel test = -8.12, n=1271, p<0.001; Fig. 1) and second broods did not differ between study sites (Cox-Mantel test = -1.16, n=723, p>0.25). Simultaneously, in outbuildings survival rate in first broods was higher than in second broods (Cox-Mantel test =2.62, n=953, p<0.009). The inverse result was obtained in bunkers, where survival rate in second broods was higher than in first broods (Cox-Mantel test = -3.39, n=1041, p<0.001; Fig. 1).

The differences in survival rate of nest contents (eggs/nestlings) between study areas and between broods were mostly determined at the hatching stage of nestlings (Fig. 2).

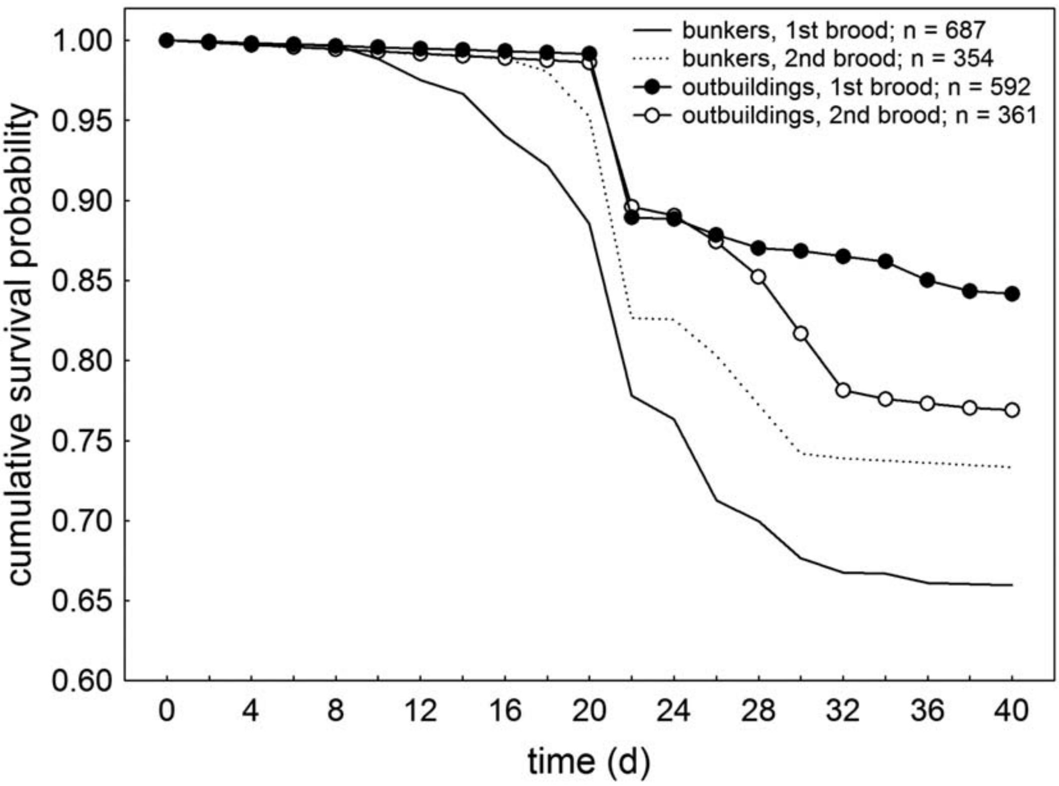

Fig. 1. – Differences in survival probability (survival curves) of Barn Swallow eggs and nestlings from first and second broods in bunkers and farm outbuildings.

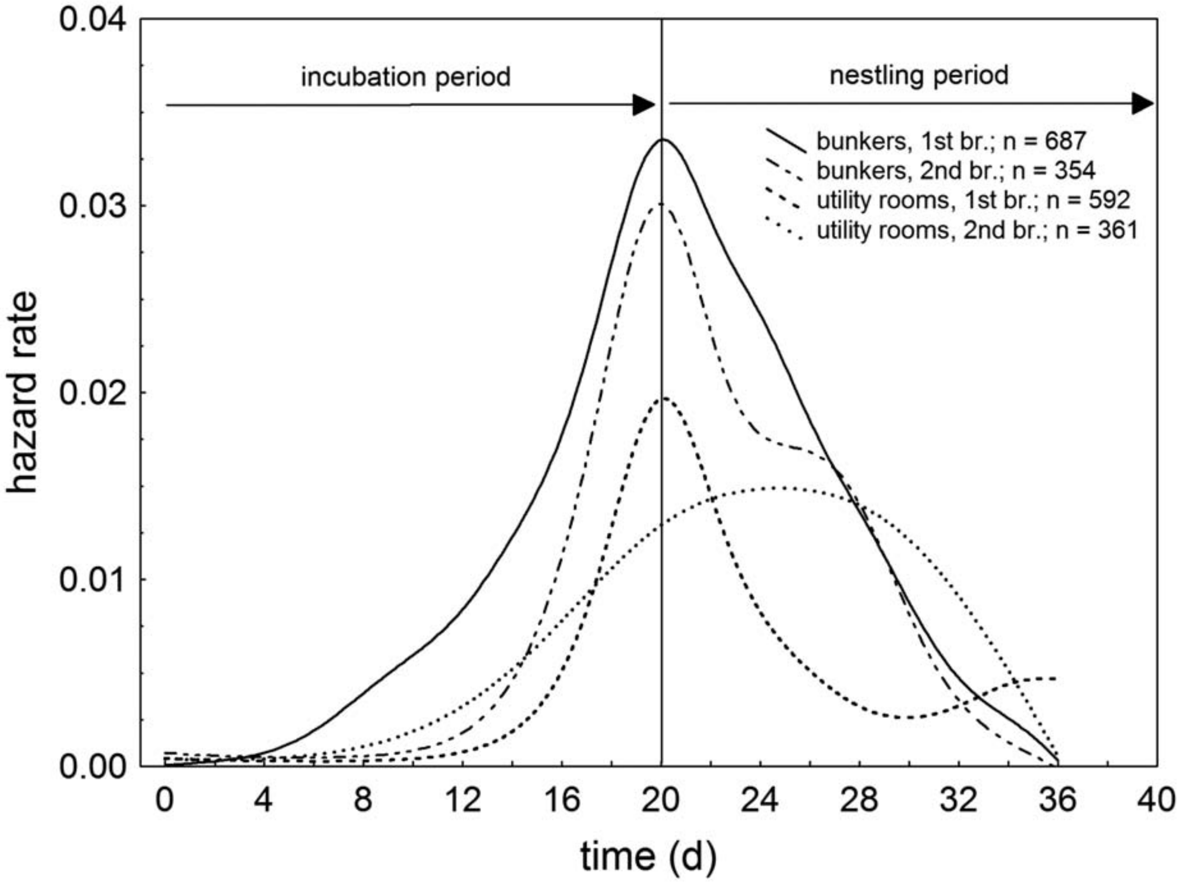

Fig. 2. – Hazard rate in the following days of egg and nestling life from first and second broods in bunkers and farm outbuildings; the curves are fitted using the distance weighted least squares smoothing technique; time in days since laying of the first eggs in clutches.

DISCUSSION

This study showed that bunkers constitute suitable and relatively good quality alternative habitats for the Barn Swallow but they are poorer nesting places than farm outbuildings. Time of breeding and mean clutch size in both broods did not differ between study areas. However, mean survival rate of nest contents (eggs/nestlings) was higher in farm outbuildings than in bunkers but the differences concerned first broods only. The results are most probably the effect of different conditions occurring in these two kinds of nesting habitat, perceptible especially at the beginning of the breeding season. At this time, weather conditions are often unfavourable (low temperatures connected with high precipitation) and are much more changeable than in later stages of the breeding season, when the temperatures are higher and much more stable. In the incubation period, during rainy and cold days, females more often have breaks from foraging and as a result of the thermal conditions prevailing inside the bunkers there is an increased risk of eggs cooling than in the farm outbuildings. This may reduce hatching success (e.g. WILLIAMS & RICKLEFS, 1984; REID et al., 1999) or can negatively influence post-hatch growth (SOCKMAN & SCHWABL, 1998) and thereby nestling survival. Unfavourable weather conditions also have an influence on insects (TURNER, 2006) and force adults to go further from the nest to localised feeding sites (BRYANT & TURNER, 1982). Adults spending more time on foraging can have a negative effect on small nestlings, especially in bunkers. Pigsties or cowsheds protect incubating females, their eggs and small nestlings better and have much more stable thermal conditions than bunkers at times of low outside temperatures. Firstly, these results arise from differences in the construction between these types of buildings. Secondly, during unfavourable weather the presence of farm animals increases the temperature inside the outbuildings and provides access to flying insects. Furthermore, relatively low temperatures in the bunkers, mostly at the first stage of the breeding season, are also heightened by the presence of water. Therefore, survival of first broods reared in pigsties or cowsheds was higher than in bunkers. During the later stages of the breeding season, temperatures are higher and weather conditions are much more stable than at the beginning of the breeding season and broods are less exposed to the effects of unfavourable weather conditions. Therefore, there are no differences in survival rates between second broods reared in the two study sites. Differences in thermal conditions can also explain the results that in farm outbuildings survival rate in first broods was higher than in second broods and inversely in bunkers. The importance of nesting places' microclimate was also found in Tree Swallows (*Tachycineta bicolor*) population, where birds preferred warmer nesting places but only during the first half of the breeding season, characterized by lower ambient temperatures than the second half of the breeding season, when swallows selected nesting sites based on their availability (ARDIA et al., 2006). Authors suggest that warmer nest temperatures may provide fitness benefits, especially at the beginning of the breeding season, which also was found in this study.

The overall survival and the same breeding success can be influenced by the phenotypic quality of breeders where high-quality individuals are often more fecund than the poor-quality ones. This is also true for Barn Swallow females whose fecundity is directly related to the body condition (MØLLER, 1994). Moreover, the breeding performance can be also affected by the age and therefore the experience of breeding Barn Swallow females (BALBONTÍN et al., 2007). However, it seems not to be the case in this study. Unfortunately, the quality of breeders was not evaluated and their age is unknown, but there were no differences in breeding time and clutch size between the two kinds of nesting places. It would seem that parental quality and quality of birds in general does not differ between bunkers and outbuildings. Therefore, the thermal conditions occurring inside the nesting places are most probably the main factor influencing the differences in survival between study areas. The significance of thermal conditions on the survival in both study sites also is supported by the estimated hazard functions. In the case of both study areas, the hazard rate was the highest in the period of nestlings' hatching. However, higher values for this period were recorded in bunkers than in outbuildings. Such results suggest that the incubation and hatching periods are the most critical moments in reproduction and determine the higher overall reproductive output of barn swallows in bunkers than in outbuildings.

The effect of different kinds of nesting place on breeding success was found also for other bird species, where natural cavities were compared with nest boxes (e.g. PURCELL et al., 1997, ROBERTSON & RENDELL, 1990, EVANS et al., 2002, CZESZCZEWIK, 2004). Nest boxes are often cleaner, dryer and warmer than natural holes. On the other hand, they are more visible and broods are more exposed to predators. The study has shown that differences in microclimate can exist also between the unnatural nesting places such as bunkers and outbuildings used by Barn Swallows as nesting places, and these determine the differences in the breeding output.

Studying the differences in breeding output of swallows between two kinds of nesting habitats, local adaptations and possible differences in the trade-off between fecundity (expressed here as number of eggs laid) and survival need to be taken into account. One of the possible adaptations to poor nesting conditions could be, for example, an investment in a smaller but better surviving brood. Because the clutch size did not differ between nest-site habitats but differed only in survival rate, no clear trade-off between the fecundity and survival in this study was found.

In conclusion, bunkers offering worse conditions for breeding than farm outbuildings, nevertheless provide a suitable and good quality alternative nesting habitat for Barn Swallows, where they achieve a relatively high breeding output, which is important for local populations of this species to survive. In the light of the mentioned declining numbers of the Barn Swallow during recent decades, all the atypical nesting places used by this species with success, such as the studied bunkers, should be protected. This is especially important in areas where the access to typical nesting places has strongly decreased over recent years. In the case of Poland, this is a result of access to European Union and restrictive regulations about animal husbandry.

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