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Do Barn Swallows (*Hirundo rustica gutturalis*) prefer to breed in inhabited houses in South Korea?

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ABSTRACT—Nest site selection is critical for reproductive success in birds. Several bird species including Barn Swallow (*Hirundo rustica gutturalis*) typically nest near human settlements, presumably because this reduces their risk of predation. Here, we investigated the nesting habits of Barn Swallows in South Korea. We predicted that abandoned houses would not be chosen even if these houses provided similar nesting conditions compared to occupied houses. We conducted surveys across South Korea and recorded human occupancy, house structure, the number of active and old nests, and the deterioration condition of houses. Among the recorded active nests, 95% were located in inhabited houses ($n = 38$), whereas only 5% were observed in abandoned houses ($n = 2$). Interestingly, human presence was a significant factor in the occurrence of active nests, whereas house structure had no appreciable effect. Among the nest site characteristics, the number of old nests was significantly higher in inhabited houses than in abandoned houses. Further, ~97% of inhabited houses were not damaged, whereas 50% of the abandoned houses were damaged, potentially affecting the nesting site selection of Barn Swallows. Our results are consistent with our hypothesis that Barn Swallows prefer to nest in human-inhabited houses. As house structures suitable for nesting are reduced due to rapid urbanization, and as swallow nests are actively eliminated by human residents, the reproductive success of Barn Swallows in South Korea can be significantly reduced. *Received 12 September 2021. Accepted 26 September 2022.*

Key words: abandoned house, conservation, Hirundinidae, human habitation, nesting ecology, northeast Asia.

Las golondrinas *Hirundo rustica gutturalis*, ¿prefieren reproducirse en casas abandonadas en Corea del Sur?

RESUMEN (Spanish)—La selección de sitio de anidación es crítica para el éxito reproductivo de las aves. Varias especies de aves, incluyendo golondrinas *Hirundo rustica gutturalis*, anidan cerca de asentamientos humanos, posiblemente porque esto reduce su riesgo de depredación. Aquí estudiamos los hábitos de anidamiento de golondrinas *Hirundo rustica gutturalis* en Corea del Sur. Predecimos que las casas abandonadas no van a ser elegidas, aun cuando esas casas ofrecen condiciones de anidamiento similares a las casas habitadas. Hicimos búsquedas en Corea del Sur y registramos ocupación humana, estructura de la casa, número de nidos activos y la condición de deterioro de la casa. De los nidos activos registrados, 95% se encontraban en casas habitadas ($n = 38$) mientras que solo el 5% se observaron en casas abandonadas ($n = 2$). Interesantemente, la presencia humana era un factor significativo en la presencia de nidos activos, mientras que la estructura de la casa no tenía efecto importante. De las características del sitio de anidación, el número de nidos viejos era significativamente superior en casas habitadas que en casas abandonadas. Además, 97% de las casas habitadas no presentaban daños, mientras que el 50% de las casas abandonadas estaban dañadas, afectando potencialmente la selección de sitio de anidación de las golondrinas *Hirundo rustica gutturalis*. Nuestros resultados concuerdan con nuestra hipótesis de que las golondrinas *Hirundo rustica gutturalis* prefieren anidar en casas habitadas. Por la reducción de las casas con estructuras aptas para la anidación de golondrinas por la urbanización rápida y por la eliminación activa de nidos de golondrina por los residentes humanos, el éxito reproductivo de las golondrinas *Hirundo rustica gutturalis* en Corea del Sur podría reducirse significativamente.

Palabras clave: casa abandonada, conservación, ecología de anidación, habitación humana, Hirundinidae, noreste asiático.

Nest site selection is directly related to nest predation, food availability (Coulson 2002), and microclimate conditions (Robertson 2009) and is therefore one of the most important determinants of reproductive success (Martin and Roper 1988, Badyaev et al. 1996, Clark and Shutler 1999, Müller et al. 2005, Doerr et al. 2006). Several bird species, including Barn Swallow (*Hirundo rustica*), House Martin (*Delichon urbicum*), House Sparrow (*Passer domesticus*), Great Tit (*Parus major*), and Common Wood Pigeon (*Columba palumbus*), habitually nest near human settlements, presumably because this reduces the risk of predation (Møller 2010). However, only a few studies have evaluated whether human presence is directly linked to nesting site selection in birds.

Several studies have investigated close associations between nesting Barn Swallows and humans. Møller (2010) suggested that breeding near human habitation is a way of reducing predation risk to nestlings, thus increasing reproductive success. According to a nest predation experiment, swallow nests built in residential buildings are protected from nest predators such as corvids, as these predatory birds avoid entering

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human-inhabited areas (Møller 2010). This is further supported by a significant difference in nest predation rate within (1.0%) and outside (23.5%) residential areas (Møller 2010). Alternatively, Liang et al. (2013) suggested that indoor nesting could be a behavioral adaptation for birds to avoid nest parasitism from species such as the Common Cuckoo (*Cuculus canorus*). Egg rejection experiments have also demonstrated that rejection rates in Barn Swallows were significantly higher in China, where this species commonly nests outside residential areas, compared to Europe, where swallows nest almost exclusively within residential areas (Liang et al. 2013).

The nesting ecology of Barn Swallows is particularly interesting because it closely matches global human distribution (Turner 2010, Scordato and Safran 2014). The presumed ancestral breeding sites of Barn Swallows were likely caves or rock exposures in mountain areas or large hollow trees (Turner 2010), and these conditions are still found in the natural breeding sites of Barn Swallows in Hainan and Heilongjiang, China (Liang et al. 2013). A recent study suggested that this species has coevolved with humans since a bottleneck event that occurred ~7,700 years ago, when the first artificial structures appeared (Smith et al. 2018). Today, Barn Swallows nest mainly in artificial structures such as barns, bridges, culverts, porches, outhouses, sheds, or residential houses (Snow et al. 1998). Further, these birds are well adapted to human presence, as demonstrated by their ability to breed in inhabited houses and stores in Japan (Ringhofer and Hasegawa 2014).

In this study, we focused on the nesting ecology of a Barn Swallow subspecies, *H. rustica gutturalis*, in South Korea. Although the Barn Swallow is not threatened or endangered in South Korea, the populations of this bird have plummeted in recent years (Koh et al. 2010), with particularly abrupt population declines in large cities (e.g., the metropolitan Seoul area; Koh et al. 2010). Barn Swallows generally make their nests in human-occupied houses in rural areas in South Korea (Lee 2009, Koh et al. 2010, Kim and Oh 2017). Over the years, rural populations have decreased across South Korea, leaving many traditional houses unoccupied. This provides a unique opportunity to evaluate whether Barn Swallows prefer nesting in seemingly similar houses with or without human presence. Here, we hypothesized that human presence is an important factor of nesting site selection in Barn Swallows, which we sought to evaluate by comparing the presence of active nests in occupied and abandoned houses. We predicted that the Barn Swallows would prefer occupied houses over unoccupied houses for nest site selection.

Methods

Study area

We conducted our study in South Korea (Fig. 1). Barn Swallows are distributed throughout the country and are typically found in low-lying open fields and farmlands during the breeding season (Lee 2009, Ismail et al. 2020). We conducted field surveys in selected residential areas in 8 provinces (Gyeonggi, Gangwon, South Chungcheong, North Chungcheong, South Jeolla, North Jeolla, South Gyeongsang, and North Gyeongsang), 1 metropolitan city (Incheon), and 1 special self-governing province (Jeju) in South Korea from 2015 to 2016 (Fig. 1). We conducted surveys during the breeding season of Barn Swallows in Korea (April–August; Kim and Oh 2017).

Monitoring methodology

We conducted opportunistic daytime nest monitoring and implemented convenience sampling (Etikan et al. 2016) to identify active breeding nests considering the cost-effectiveness and practicality of this approach (Battaglia 2008). We used the presence of foraging individuals to locate the general habitats of Barn Swallows, and thus the general area of nesting sites, as food availability plays an important role in determining suitable nesting sites for breeding pairs (Ringhofer and Hasegawa 2014). Once we spotted foraging individuals, we randomly surveyed houses in the surrounding area to find active nests (Ambrosini et al. 2002). Here, we defined "active nests" based on the following criteria: (1) a nest with adults incubating eggs or rearing chicks at the time of observation, and (2) a nest with fresh feces or eggshells accumulated at the bottom.

After locating active nests, we recorded the occupation status of houses where the nests were located, depending on whether the houses were inhabited by humans or not. We classified the houses as "inhabited" or "abandoned," and

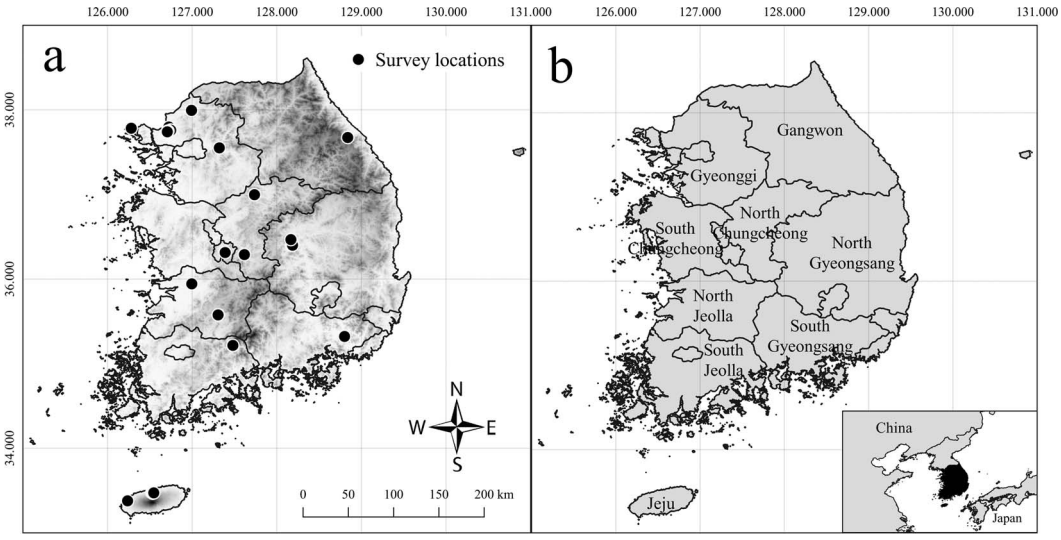

Figure 1. South Korean survey locations (black dots) are shown in (a), and provincial names are shown in (b). The inset map shows the location of South Korea in northeast Asia, with the study extent highlighted in black. The elevation raster layer downloaded from WorldClim (https://www.worldclim.org/) was used as the base map in (a).

defined inhabited houses as those houses with confirmed and continued human residence during the survey period. Similarly, we defined abandoned houses as those without any human residents or regular visitors. To evaluate the factors potentially affecting nest site selection, we recorded the following 3 characteristics for each house: (1) number of active and old nests, (2) house structure, and (3) deterioration condition of the house. Old nests that have been used previously are known to be used repeatedly by nesting Barn Swallows and may act as an important cue for nest building (Safran 2006). Here, we defined the number of old nests as the total number of old nests recorded separately for inhabited and abandoned houses.

The structure of houses reflects the regional climatic characteristics (Lee 2002), and therefore we presumed the sampling of house structures to also broadly reflect the macro- and micro-climatic environments for nesting. Based on the overall shapes, we defined the house structures as "L-shape," "square-shape," "I-shape," or "C-shape" (Fig 2). The deterioration condition was recorded as "not damaged," "partially damaged," "more than 50% damaged," or "completely damaged." We recorded deterioration condition of houses because we presumed that, because Barn Swallows

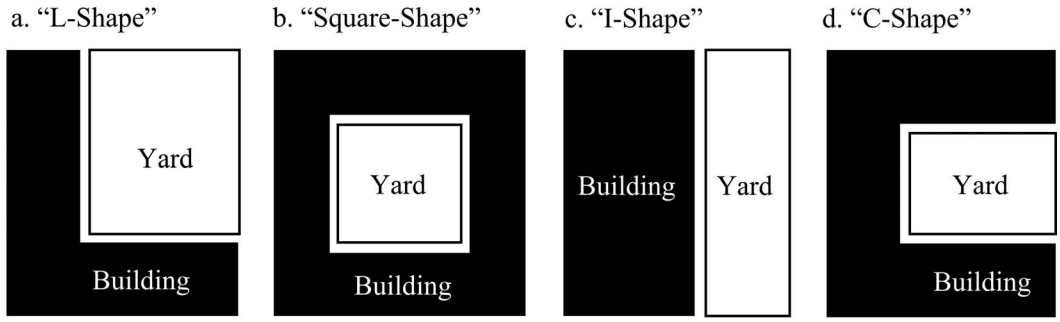

Figure 2. The general shapes of traditional house structures in South Korea. Among these structures Barn Swallows are usually found nesting in square- (b) or I-shaped (c) houses.

Table 1. Barn Swallows nesting in inhabited and uninhabited houses in South Korea. Number of inhabited houses and abandoned houses within a 200 m radius from the inhabited houses observed in each of the studied provinces.

Province	Number of inhabited houses	Number of abandoned houses	Total
Gyeonggi	16	27	43
Gangwon	1	1	2
South Chungcheong	1	4	5
North Chungcheong	3	9	12
South Jeolla	3	7	10
North Jeolla	3	5	8
South Gyeongsang	2	14	16
North Gyeongsang	4	18	22
Jeju	4	6	10
Incheon	1	18	19
Total	38	109	147

nest in close associations with humans (Zink et al. 2006), highly deteriorated houses may be selected less frequently for nesting compared to intact or slightly deteriorated houses. After detecting active nests, we randomly sampled abandoned houses located within a 200 m radius of each house with active nests, which corresponds to the mean foraging distance of Barn Swallows (Ringhofer and Hasegawa 2014). The characteristics of abandoned houses were evaluated in the same way as described above. The data we collected during 2 breeding seasons broadly covered South Korea. However, the sampling of survey sites was not repeated in both years due to the opportunistic nature of the surveys.

Statistical and spatial analyses

We first performed a chi-square test to investigate whether nest activity was related to the occupation status of houses. We conducted a Spearman's rank correlation test to determine whether the number of old nests, the deterioration condition, and the structure of houses were correlated with the nest activity. We also conducted Spearman's rank correlation test on the number of old nests and deterioration condition. A Kruskal-Wallis test was conducted to compare the number of old nests between inhabited and abandoned houses, as well as between types of house structures. Finally, we conducted a chi-square test on a contingency table to test the correlation between the occupation status of houses and the structure and deterioration condition of houses. All statistical analyses were performed in R 4.1.3 (R Core Team 2022) using RStudio (RStudio, Inc.).

We also conducted spatial analyses to estimate the distances between abandoned and inhabited houses to nearest agricultural lands, respectively. For these analyses, we used the agricultural landscapes (rice paddies and dry agriculture) extracted from a fine-scale (10 m resolution) land cover map provided by the Ministry of Environment (https://egis.me.go.kr/). We selected agricultural landscapes for the analyses as these are the primary foraging grounds of Barn Swallows (Orłowski and Karg 2013). Next, we estimated the distances between abandoned and inhabited houses to investigate the potential distance effects between the 2 house types. We conducted spatial analyses using the "Near" tool in ArcMap 10.8.1 (ESRI, Redlands, California, USA).

Results

Nest site selection in inhabited and abandoned houses

In total, we investigated 147 houses during nest monitoring (Table 1; Fig. 1a). Of these, 38 houses were inhabited and 109 were abandoned. The 109 abandoned houses had a mean distance of 88 m away from the 38 inhabited houses. Inhabited houses were generally significantly closer to agricultural lands (mean = 60 m) compared to abandoned houses (mean = 9.7 km). Out of 40 active nests, 95% (n = 38) were located in inhabited houses, whereas only 5% ($n = 2$) were located in abandoned houses. The number of active nests was significantly different between the inhabited houses and abandoned houses (χ^2 = 32.4; df = 1; $P < 0.001$).

Nest site characteristics in inhabited and abandoned houses

The results of Spearman's rank correlation tests showed a positive correlation between nest activity and the number of old nests ($r = 0.52$; $S = 253{,}938$; $P < 0.001$) and a significantly negative correlation between nest activity and the deterioration condition ($r = –0.43$; $S = 758{,}995$; $P < 0.001$). Among the 40 active nests we recorded, 26 were in I-shaped houses, 10 were in square-shaped houses, 3 were in C-shaped houses, and 1 was in an L-

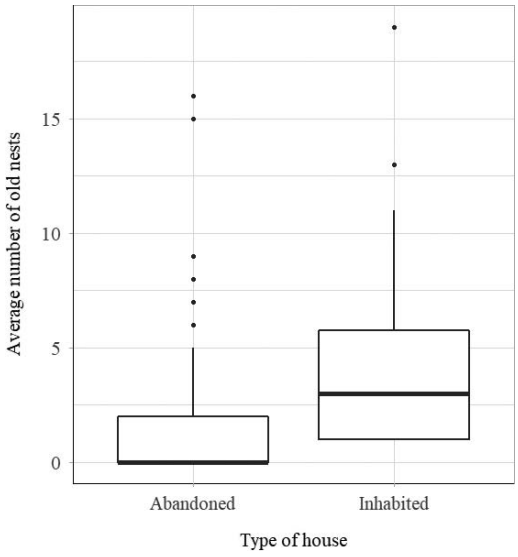

Figure 3. Distribution of the number of Barn Swallow old nests (total $n = 332$) in inhabited ($n = 168$) and abandoned ($n = 164$) houses in South Korea. The numbers of old nests were significantly different between the types of houses according to the Kruskal-Wallis test ($P < 0.001$).

shaped house. Although more active nests were recorded from I-shaped houses, the overall correlation between nest activity and house structure was not significant ($r = 0.10$; $S = 47{,}798$; $P = 0.242$). The correlation between the number of old nests and the deterioration condition showed a significantly negative correlation ($r = –0.25$; $S = 659{,}927$; $P = 0.003$). Among the old nests recorded in inhabited houses, 98.8% ($n = 166$) were in houses that were not damaged, and 1.2% ($n = 2$) were in houses that were partially damaged. In contrast, among the old nests recorded in abandoned houses, 45% ($n = 73$) were in undamaged houses, 26% ($n = 42$) were in partially damaged houses, 23% ($n = 38$) were in houses with greater than 50% damage, and 6% ($n = 11$) were in completely damaged houses.

Of the total number of old nests recorded during surveys ($n = 332$), 168 were in inhabited houses and 164 were in abandoned houses. We found a mean of 1.5 ± 2.9 old nests in abandoned houses (all values mean ± SD), and a mean of 4.42 ± 4.2 old nests in inhabited houses (Fig. 3). The number of old nests was significantly greater in inhabited houses than in abandoned houses (Kruskal-Wallis $\chi^2 = 37.028$; df = 1; $P < 0.001$; Fig. 3). The number of old nests was correlated with house structure (Kruskal-Wallis $\chi^2 = 34.015$; df = 3; $P < 0.001$). Specifically, the square- and I-shaped houses had 4–7 times more old nests than L- and C-shaped houses. Among the houses surveyed during our study, 60% were I-shaped, 18% were square-shaped, 15% were L-shaped, and 7% were C-shaped ($n = 147$). The correlation between the occupation status and structure of houses was not significant ($\chi^2 = 6.5639$; df = 3; $P = 0.087$).

The deterioration condition of houses was correlated with their occupation status ($\chi^2 = 26.558$; df = 3; $P < 0.001$). While 97% of inhabited houses exhibited no damage, only 50% of the abandoned houses were undamaged. Further, 27% of the abandoned houses were partially damaged, 16% were mostly damaged (>50%), and 7% were completely damaged. Only 3% of the inhabited houses were partially damaged but no greater conditions of deterioration were recorded.

Discussion

Consistent with our initial hypothesis, our results suggest that Barn Swallows nest preferentially in human-inhabited houses in South Korea, with up to 95% of active nests recorded in inhabited houses. The 2 abandoned houses where active nests were observed were flanked by stores that were located in a busy market with constant human activities. Even if the houses themselves were abandoned, these 2 nests were very close to human activity. In contrast, we have never observed active Barn Swallow nests in completely abandoned houses with no human activities around them (DJ and BL, pers. obs.). Many bird species are known to breed in artificial structures, and have successfully adapted to human presence (Mainwaring 2015). Despite the correlation between the nesting habits of Barn Swallows and human presence, there are few studies that have directly investigated the breeding success associated with humans (Møller 2010). Our results therefore provide additional evidence for close associations between human habitations and nesting site selection of Barn Swallows (Møller 2010, Turner 2010, Liang et al. 2013, Ringhofer and Hasegawa 2014), consistent with previous studies linking

human presence to the nesting of Barn Swallows (Hayashi et al. 2020).

In general, we recorded more old nests in inhabited houses with active nests. This is likely because the number of old nests acts as an important cue for nesting in breeding Barn Swallows (Safran 2006). Previous studies have also demonstrated that old but intact nests are recurrently used by nesting Barn Swallows, thereby reducing the cost of building new nests (Ringhofer and Hasegawa 2014). Thus, Barn Swallows seem to prefer inhabited houses for nesting with preexisting old nests acting as cues for nesting. Furthermore, in our study area, the close proximity of inhabited houses to major foraging habitats may afford additional benefit of high relative prey abundance.

In this study, the deterioration condition of houses was negatively correlated with the number of old nests. This is likely because inhabited houses receive regular maintenance by human residents, thus having a generally lower degree of deterioration. Such regular maintenance, in turn, may provide long-term nesting sites for Barn Swallows, given the nests are not removed by human residents. However, the lower frequency of old nests in abandoned houses could also be due to the loss of old nests caused by structural deterioration.

We initially hypothesized that the structure of houses would reflect the regional climatic characteristics (Lee 2002), thus providing both macro- and micro-climatic environments for nesting. However, our results show that the structure of houses was not related to the nesting of Barn Swallows. This likely implies that Barn Swallows may use finer-scale cues other than the overall house structure for nesting (Ambrosini and Saino 2010). Based on the known breeding ecology of Barn Swallows (Hasegawa et al. 2010, Pagani-Núñez et al. 2016) and our long-term observations on nesting Barn Swallows in Korea, one of the most likely "fine-scale cues" may be the roof eaves. As roof eaves can provide protection against predators and adverse weather conditions (Lee 2002, Turner 2010), they may provide significant benefits to the reproductive success of Barn Swallows. However, not all houses with roof eaves are selected for nesting, suggesting Barn Swallows may rely on multiple factors to select nesting sites. Therefore, the eventual selection of nesting site may result from complex trade-offs between climatic and topographic conditions, predation pressure, brood parasitism, food availability, and pre-existing nesting cues (Blomqvist and Johansson 1995, Tieleman et al. 2008).

Based on our results and previous studies on the ecology of Barn Swallows, we suggest several reasons for the close association between human habitation and nesting Barn Swallows in Korea. The first reason is the general breeding ecology of the Korean Barn Swallow population. In contrast to the colony-nesting populations of Barn Swallows (Shields and Crook 1987, Fujita and Higuchi 2007), the Korean Barn Swallow populations breed solitarily (Ringhofer and Hasegawa 2014). Previous studies have demonstrated the reduction of predation risk through colony-living in Barn Swallows (Møller 1987) and related species (e.g., in Bank Swallow [*Riparia riparia*]; Hoogland and Sherman 1976). For example, Møller (1987) demonstrated that larger Barn Swallow colonies were able to detect predators faster and had low predation risk (1–2% on average). On the other hand, disadvantages of coloniality included increased frequency of brood parasitism and increased ectoparasite infestation (Møller 1987). Although Barn Swallows in Korea do not nest in large colonies, it may be possible for them to attain some benefits of coloniality (e.g., reduced predation) by living close to humans, and thereby increase their breeding success. The second reason is the shape of the nest. Some hirundinid species such as the Red-rumped Swallow (*Cecropis daurica*) and the House Martin, which are known to be less dependent on human presence when nesting, make closed cup-shaped nests with a narrow opening at the top (Winkler and Sheldon 1993). This narrow opening reduces brood parasitism and predation (Liang et al. 2013), and such closed nest shapes are important for avoiding predators and brood parasites in a wide variety of avian taxa (Feeney et al. 2012). However, Barn Swallows construct open cup-shaped nests that are more vulnerable to brood parasitism and predation (Liang et al. 2013). We thus presume that Barn Swallows may be able to reduce the risks of having open nests by living close to humans and building nests under roof eaves. In addition, there could be differences in resource availability between inhabited and abandoned houses. For example, the diversity and richness of insect prey

could be different between inhabited and abandoned houses, potentially related to different degrees of human activities and associated differences in landscape types (Abella-Medrano et al. 2015). However, such data is not available for the country at present.

Nesting site selection in Barn Swallows likely involves multiple factors at different scales, and additional research is needed to further clarify other effects of human presence on the nesting site selection in this species. For example, our data included abandoned houses ($n = 109$) within a 200 m radius of a breeding nest ($n = 38$), with the radius based on the mean foraging distance of Barn Swallows (Ringhofer and Hasegawa 2014). However, it was not possible to survey every inhabited house in the survey area due to time and resource constraints, although we visually verified the presence of additional inhabited houses with active Barn Swallow nests. Nevertheless, the sampling design was based on our long-term (~20 years) observations that Barn Swallows predominantly make nests in, or in close proximity to, inhabited houses, and that Barn Swallows often abandon their nests once the house becomes abandoned by human residents (DJ and BL, unpubl. data). We therefore focused primarily on sampling abandoned houses within the same 200 m radius of active nests we surveyed for comparative purposes. While ideal sampling would include all the breeding nests in inhabited houses within a given 200 m radius area, our data still suggest significant associations between human presence and nesting site selection of Barn Swallows even with a much larger sample size of abandoned houses (for example, significantly more active nests were found in inhabited houses compared to abandoned houses).

Additional studies with denser spatial sampling and additional variables such as the degree of urbanization, resource availability, and the number of predators may provide further insights into the associations between human presence and nesting site selection of Barn Swallows. Future studies could also conduct comparisons between different Barn Swallow populations that nest in different degrees of human presence (Snow et al. 1998). Therefore, the relationships between human presence, nesting site selection, and reproductive success warrant further investigation, and our study provides baseline information on the association between human presence and nesting site selection in Barn Swallows.

The nesting habits of Barn Swallows have implications for their conservation given the close association between nests and human habitation. Especially in Korea, urbanization is ongoing at a rapid pace (Lee and Miller-Rushing 2014), leading to large-scale degradation of foraging habitats suitable for Barn Swallows (Borzée et al. 2019). Along with the overall degradation of habitats, urbanization has also caused changes to the types of houses, usually the conversion of traditional or single-story houses (which are generally used by Barn Swallows for nesting) into multi-story apartments mostly unsuitable for nesting Barn Swallows. Furthermore, while Barn Swallows have been traditionally regarded as a symbol of good fortune in Korea, human residents may still actively remove the nests of Barn Swallows due to the feces that accumulate near active nests, further impacting the reproductive success of populations (Kim 2017). Therefore, effective educational outreach and conservation programs are needed to better resolve conflicts between nesting Barn Swallows and human residents. Such activities may provide educational programs to village residents and can also include installments of artificial nests (Teglhøj 2018) and holders to collect feces. Such programs will be invaluable for the effective long-term conservation of this iconic species.

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