Acta Zoologica Academiae Scientiarum Hungaricae 69(1), pp. 63–72, 2023
DOI: 10.17109/AZH.69.1.63.2023

NEST ENTRY SHAPE CHANGE MAY CAUSE NEST ABANDONMENT IN URBAN CAVITY-NESTING SPECIES: A CASE STUDY OF THE TREE SPARROW *PASSER MONTANUS*

Ju-Hyun Lee[1], Se-Yeong Kim[2], Dae-Han Cho[2] and Ha-Cheol Sung[1]*

[1]*Department of Biological Sciences, Chonnam National University,*
Gwangju, 61186, Republic of Korea
E-mail: birdscholar351@gmail.com; https://orcid.org/0000-0002-1288-3336
*E-mail: shcol2002@jnu.ac.kr; https://orcid.org/0000-0002-7494-7446 (*corresponding author)*
[2]*School of Biological Sciences and Biotechnology, Chonnam National University,*
Gwangju, 61186, Republic of Korea
E-mail: goatmxj4010@naver.com; https://orcid.org/0000-0003-3197-3203
E-mail: kk_216@naver.com; https://orcid.org/0000-0002-8961-7159

The threat of predation is the main cause of bird nest abandonment, with such behaviour imposing considerable energetic costs on breeding birds. However, for several species, nest abandonment can be a less costly alternative to complete brood failure. In this study, we examined nest abandonment among Eurasian Tree Sparrows (*Passer montanus*) by surveying 71 Tree Sparrow nests with various types of entry holes and conducted artificially manipulating some of the entrance shapes. We found that nest abandonment was caused by changes to the nest entry shape in seven cases and by human interference in two cases. Nest abandonments occurred throughout the breeding season, and breeding pairs attempted to breed again immediately after nest abandonment. The results of the artificial nest entry shape manipulation experiment showed that nine of twelve nests (75.0%) were abandoned where the nest entrance holes were widened, and six of eleven nests (54.5%) were abandoned where the nest entrance holes were narrowed. However, none of the nests were abandoned where the entry shape was unchanged. Thus, nest abandonment by Tree Sparrows is correlated with nest entry shape manipulation and is more likely to occur when the energy cost of breeding again is less than that of abandoning the nest.

Keywords: nest abandonment, nest entry shape, *Passer montanus*, secondary cavity nester, Tree Sparrow.

INTRODUCTION

In most passerine birds, nest predation is the main reason for breeding failure (Nilsson 1984, Martin 1993, Remeš *et al.* 2012). With such intense selective pressure for nesting birds as predation, many species have adapted to reduce nest predation. For example, the nests of cavity-nesting birds are less likely to suffer predation than non-cavity-nesting birds because their nest entrances are usually higher up and are more concealed (Martin & Li 1992). In particular, secondary cavity-nesting birds (i.e., non-excavators (Martin & Li 1992)) that depend on natural openings or on those created by primary cavity nesters could suffer nest failure because they use older cavities where they can be prey more extensively on old cavities (Sonerud 1985, Li & Martin 1991). Thus, nest site selection for breeding pairs is an evolutionary adaptive process that can reduce nest predation risk (Munro 2007).

Nest building, incubating, and rearing offspring impose temporal constraints and energetic costs on breeding pairs. Nest viability is significantly related to breeding success as it can keep the eggs and chicks warm and also protect against predation. However, the invested time and energy in nest building can impart a significant breeding cost (Collias & Collias 1971, Collias *et al.* 1971, Gauthier & Thomas 1993), meaning that abandoning a nest and re-building elsewhere should theoretically be a rare occurrence (Metz 1991, Stanley 2002). However, if the benefits of nest abandonment outweigh the total breeding costs, natural selection will drive breeding pairs to abandon their nest when the risk of predation is high (Berger-Tal *et al.* 2010, Flegeltaub *et al.* 2017). In other words, nest abandonment can occur when it is preferable to do so rather than risk losing eggs and nestlings to predation (Beckmann & Martin 2016, Flegeltaub *et al.* 2017).

The threat of predation during nest building or the incubation period is a major cause of nest abandonment (Vaske *et al.* 1994, Nelson & Hamer 1995, Maddox & Weatherhead 2006, Isaksson *et al.* 2007). Reduced nest concealment has been shown to increase nest predation risks in many passerine species, particularly in cavity-nesting birds (Martin & Li 1992). For example, Grey Fantails (*Rhipidura albiscapa*) tried to place nests in areas concealed by the surrounding vegetation only to abandon their nests when the predator interference occurred (Beckmann & Martin 2016, Flegeltaub *et al.* 2017). Least Terns (*Sterna antillarum*) showed higher rates of nest abandonment around the edges of breeding colonies rather than in the centre because of the higher predation rates at the edges (Brunton 1997). Wesołowski (2002) suggested that the entrance hole size of Marsh Tit nests (*Parus palustris*) did not influence overall predation risk, although nests built in old woodpecker holes or dead wood were predated more often. Therefore, building nests in more concealed areas can reduce potential predation risk, while the deformation of the nest can be expected to be accessible by potential predators.

The Eurasian Tree Sparrow (*Passer montanus*) is a small passerine bird widely distributed across the Eurasian landmass (Summers-Smith 1995). In the Republic of Korea, Tree Sparrows that live in urban areas are typical cavity nesters (Chae 2019, Lee *et al.* 2020) that favour artificial structures such as roof-tiled houses, where they may have bred in the past, over purpose-built nesting boxes (Lee *et al.* 2020). The main predators of Tree Sparrows are cats, snakes, rats, and kestrels (Summers-Smith 1995, Lee *et al.* 2020), which can often collapse the nest entrance. Reproductive failure in Tree Sparrows may occur because of predation (Cordero 1991), high ectoparasite prevalence (García-Navas & Sanz 2012), temperature changes (Pinowski 1968), and nest abandonment (Lee *et al.* 2020). Lee *et al.* (2020) observed that breeding failure in Tree Sparrows was frequently associated with nest abandonment in urban environments.

In this study, we examined the causes of nest abandonment in Tree Sparrows in urban environments using various types of nesting sites and tested whether changes in nest entry shape increased the probability of nest abandonment.

MATERIALS AND METHODS

Study area

We studied Tree Sparrows at three sites in Gwangju, Republic of Korea (Fig. 1), during breeding seasons in 2019 (Sites 2 and 3) and 2020 (Site 1). The nests were located in holes in trees, woodpeckers' nests, cracks in buildings, and holes in steel frames at Site 1; gaps between tiles in tile-roofed houses at Site 2; and artificial nest boxes (130 × 150 × 200 mm length, width, and height, respectively; hole diameter: 32 mm) at Site 3 (Fig. 1). Site 1 was located on the campus of Chonnam National University—an area of dense tree plantations in and around buildings with other potential nest competitors (hole-nesting birds, e.g., *Parus major*) and predators (cats, snakes, and kestrels, e.g., *Falco tinnunculus*) present in the area. Sites 2 and 3 were located in the city centre, where the only existing vegetation was the trees situated around the tile-roofed houses, with nest boxes installed on the trees. Only Tree Sparrows were known to breed at these sites, although cats and kestrels were also observed. During the fieldwork period, both the approach of predators and threats of predation (e.g., kestrels attacking nests, snakes approaching breeding sites) were observed, but it was difficult to confirm predation directly during the nest survey. To confirm the

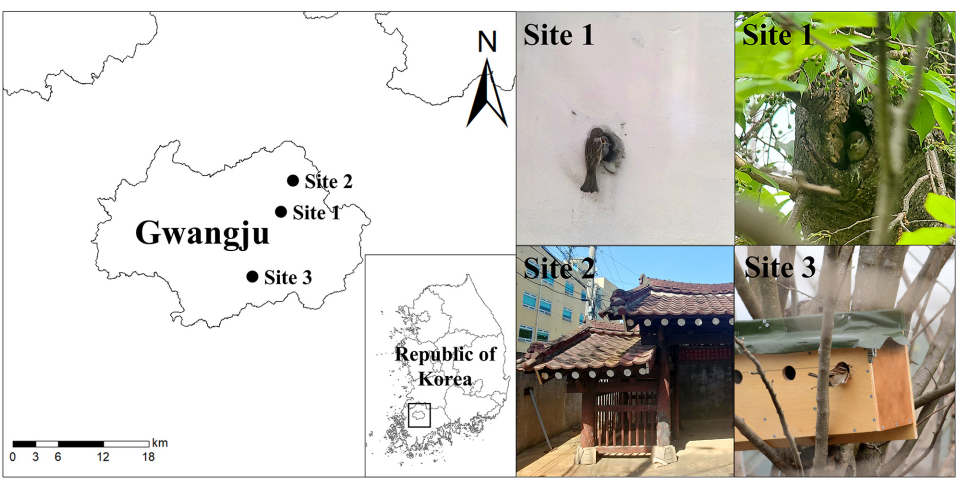

Fig. 1. Location of the study area (left) and examples of Tree Sparrow nests at the study sites (right). Site 1: Agricultural Practical Training Center, Chonnam National University, 77, Yongbong-ro, Buk-gu, Gwangju, Korea (N 35°10′31.02″, E 126°53′56.33); Site 2: 28, Uchi-ro 422beon-gil, Buk-gu, Gwangju, Korea (N 35°12′17.02″, E 126°54′7.63″); Site 3: 209–12, Ijang-dong, Nam-gu, Gwangju, Korea (N 35° 5′3.76″, E 126°51′37.93″)

re-nesting of each breeding pair, we captured adult individuals using mist nets (Avinet; 30 mm nylon mesh) and sparrow traps (Sparrowtraps.net; 24 × 16 × 8 inches) before marking them with coloured rings (Avinet; Darvic markers XF 2.3–2.5 mm). Once the birds' morphological traits had been measured, they were then released.

Nest survey

The nest survey was conducted while conducting a simultaneous study of Tree Sparrow breeding habit (Lee *et al.* 2020). We found the nests by observing and then following the adult individuals during the breeding season when they repeatedly visited the nest while collecting materials or foraging for other items. After finding the nests, we used a ladder to access them and examined the breeding status. Whenever we approached a nest to conduct a survey, the breeding pair remained approximately 15–20 m away, only re-entering the nest once we had left the site. During the nest survey, it was necessary to lift and open a roof tile, which meant that the red clay wall might collapse during this process. Each nest was examined every three days during the breeding season, and any chicks in the nests were marked with different combinations of coloured rings. The breeding status was categorized into four stages: the nest-building period, the egg-laying period, the incubation period, and the nestling period. We considered a "nest success" to be a nest with more than one fledging chick and a "nest abandonment" to be when whole clutches failed to survive due to parental abandonment (undetected predation) when non-hatched cold eggs or dead chicks were found in a nest. After the breeding was complete, we checked the shape of the nest entrance of all nests and recorded any changes caused by the nest survey process. We divided the nests into three groups according to the entry shape: unchanged, changed, and entrance collapse.

Nest entry size manipulation

The nest entrance size manipulation experiment was conducted in the gaps between the tiles in the tile-roofed houses in the same condition as those at Site 2 where nest abandonment was the most frequent during the nest survey process. The experiment was conducted between April and May 2022, at breeding sites near Hampyeong Bay (N 35° 8'30.67", E 126°24'4.73"), 50 km away from the nest survey sites. The nest entry size was measured using the ImageJ (v.1.52) program after attaching a 15cm ruler and photographing the hole. Nest entry size manipulation was assigned alternately to one of three treatments: 1) widening (n = 12), 2) narrowing (n = 11) and 3) control (n = 11), with the first nest being assigned randomly. We only selected nests that were being used for incubation in order to minimize the energetic costs to the breeding pairs after checking the inside of the nest with an endoscopic camera (Bluetec BS-99E). The nest entrance was widened by approximately 50–80% and was done by raising the roof tile, fixing it with stones, and digging out the red clay around the nest hole. For the narrowing entrance size was narrowed by approximately 50% by moving the roof tiles to reduce the entry size and covering the nest hole using any surrounding objects, only leaving space for the birds to enter the nest. The materials used (such as stones and roof tiles) were collected from the ground in a nearby area that was sufficiently far from the nests. For the control nests, we simply observed the inside of the nest with an endoscopic camera. All manipulations were completed rapidly (within 1 min), and no predators approached the nest during this time.

The researcher covered the nest entrance so that the breeding pair could not observe the manipulation process. After the experiment, we waited for the breeding pair to arrive at the nest and checked that they could enter the nest. We then revisited each nest after three days to check whether the nest had been abandoned. A Mann-Whitney U test was carried out to determine any significant differences in the nest abandonment rate between the nest entrance size manipulated group and the control group. Statistical analysis was performed using IBM SPSS statistics (v.20).

This study was approved by the Chonnam National University (CNU) and CNU Laboratory Animal Research Centre under the Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research (Approval No. CNU IACUC-YB-2022–14).

RESULTS

We monitored 71 nests in the study area and observed a total of nine abandoned nests (12.68%), two of which were at Site 1 (5.13%) and the remaining seven at Site 2 (23.33%). In seven of the nests, abandonment occurred when the shape of the nest entrance had been changed, while the other two nests were abandoned when the breeding pair directly encountered the researcher (Table 1). No chick predation was observed at the study sites. During the nest survey, changes in nest entry shape were observed in seven nests, with all respective breeding pairs abandoning their nests. Among the breeding pairs in 64 nests with unchanged nest entry shapes, 62 pairs remained in their nests, while the other two pairs abandoned their nests during the incubation period because of human encounters. Nest abandonment occurred at the beginning of the breeding season (April to May) and did not occur after the mid-breeding season (June ~). Nest abandonment occurred three times during the nestling period, three times during the incubation period, twice during the egg-laying period, and once during the nest-building period. Particularly during the nestling period, chick death was discovered after nest abandonment on Day 3, Day 6, and Day 12; chick death days were calculated based on the hatching date.

The results of the experiment showed that nest abandonments occurred significantly more often at nests where the nest entry shape was changed (15/23) than at nests where the entry shape was not changed (control group;

Table 1. Comparison of nest abandonment cases between breeding periods.

Site	No. of nests	No. of abandoned nests	No. of nest abandonment cases during breeding period			
			Nest building	Egg laying	Incubation	Nestling
Total	71	9	1	2	3	3
Site 1	39	2	1	–	1	–
Site 2	30	7	–	2	2	3
Site 3	2	–	–	–	–	–

0/11; Z = 3.53, $p < 0.05$). When the net entry shape was changed after the experiment, the breeding pair came to the nest and checked the nest hole near the entry without entering the nest. If nest abandonment occurred, the breeding pair left the nest (15/23), and if nest abandonment did not occur, the breeding pair entered the nest (8/23). Nest abandonments occurred at nine of twelve nests (75.0%) where the nest entrance holes were widened and at six of eleven nests (54.5%) where the nest entrance holes were narrowed, although there was no significant difference in abandonments between the widened and narrowed nest entry shape (Z = 1.006, $p = 0.314$).

DISCUSSION

Our results suggest that changing the nest entry shape may elicit nest abandonment because of the perceived threat of predation. Predation of Tree Sparrow nests in urban areas is very low because their nests are typically built in locations that are difficult to access (García-Navas & Sanz 2012, Lee *et al.* 2020). However, in the present study, Tree Sparrows abandoned their nests when the nest entry shape was changed, even though no nest predation occurred. This suggests that the birds may perceive a change in nest entry shape as a sign that predators have visited.

In many passerine birds, nest concealment improves reproductive success through avoiding predators, while reduced nest concealment causes increased predation pressure (Martin 1992, Beckmann & Martin 2016). Nest abandonment is an anticipative response to perceived potential nest predation because it is more advantageous to simply abandon and construct a new nest (Berger-Tal *et al.* 2010). Among the study areas, nest abandonment occurred most frequently at Site 2, where the nest entrances were easily deformed, while nest abandonment was rare at Site 1 and did not occur at Site 3. Nest holes at Site 2 were located in areas where the buildings had roof tiles and red clay walls that were prone to collapse, with the Tree Sparrows attempting to nest in the gaps under the tiled roof. Tree Sparrows abandoned their nests when the shape of the entry hole was changed after visits by the researchers, with the breeding pairs re-establishing a new nest nearby and attempting to breed again. However, after the researchers changed the nest surveying method to open the roof tile at the top of the nest without touching the nest entrance, nest abandonment behaviour ceased. Conversely, the entrances of the nest holes at Site 1 were difficult to alter since they mainly consisted of woodpecker holes in trees and building gaps. Thus, nest abandonment only occurred due to human encounters at the nest or when the entrance hole was deformed due to the collapse of a wall. In addition, the reason why nest abandonment was not observed at Site 3 was that nest boxes were provided. At Sites 2 and 3, although the researchers continued to survey the nests, and the breeding pairs continued to be alert near the nests, nest abandonment was almost absent. Similarly, an experiment on nest abandonment by Grey Fantails during nest construction showed that 67% of the breeding pairs abandoned their nests when mock predators (Pied Currawong; *Strepera graculina*) were placed near the nesting site. However, none of the breeding pairs abandoned their nest when a mock non-predator (King Parrot; *Alisterus scapularis*) was used (Berger-Tal *et al.* 2010). One study showed that Grey Fantail nest abandonment is most frequent during the early stages of nest construction when the nests are not well concealed (Beckmann & Martin 2016). The Prairie Warbler (*Dendroica discolor*) also abandons its nest when threatened by predators during nest construction (Nolan 1978). At the site of the current study, Tree Sparrows only entered their nest after approaching the entrance and examining the shape; they only abandoned the nest if the nest entry shape was changed. In summary, the breeding pairs abandoned their nest when perceiving that the nest may have been exposed to predators, with nest entry deformation being the primary factor for abandonment.

The threat of predation is a major factor in the reproductive failure of breeding pairs across many bird species. In particular, nest concealment directly influenced nest predation risk in passerines, with a lower concealment rate associated with increasing nest predation risk (Martin 1992, Beckmann & Martin 2016). Artificial experiments manipulating the nest entry shape showed that nest abandonments of Tree Sparrows only occurred at nests where the nest entry shape was changed and occurred more often when the entrance had been widened. The main predators of Tree Sparrows are snakes, cats, and humans (Summers-Smith 1995). When a predator invades the nest, the nest entry shape could be changed, so it could be regarded by the breeding pairs as being a threat of predation. In addition, a change in the nest entry shape could indicate potential predation (including humans), and it was predictable that nest abandonment would occur to reduce the breeding cost.

Nest abandonment by Tree Sparrows occurred throughout the entire breeding period. During the foraging period, in particular, the breeding pair left the chicks to die after the nest entry shape was changed, even though the chicks were beginning to sprout feathers (day 12; see Lee *et al.* 2020). The breeding pair would then attempt to breed again under a nearby roof tile a short time later. In general, nest abandonment occurred during the nest-building period and, more rarely, during the early incubation period; it rarely occurred during the late incubation period (Munro 2007, Beckmann & Martin 2016, Flegeltaub *et al.* 2017). Nest abandonment is rarely observed in birds during the nestling period because the cost of rearing the young outweighs the benefits of nest abandonment (Gauthier & Thomas 1993, Eggers *et al.* 2006, Berger-Tal *et al.* 2010). For example, Grey Fantails mainly abandoned their nests during the nest-building stage (Berger-Tal *et al.* 2010, Beckmann

& Martin 2016). According to Bordjan and Tome (2014), nest abandonment by Great Tits mainly occurred during the incubation period (69% of 35 cases), and sometimes during the early nestling stage (20%). According to Verboven and Tinbergen (2002), nest abandonment rates decline markedly as the incubation period progresses as increased investment in the original nest reduces the parents' ability to produce a new clutch (see Slagsvold 1984).

Birds may abandon reproduction attempts if the costs exceed the expected benefits and attempt to compromise present risk and future reproductive success (Williams 1966, Verboven & Tinbergen 2002). In response to potential predators, nest abandonment behaviour may be an adaptive strategy where abandoning the nest and initiating a new nest are more profitable than maintaining a potentially compromised nest (Berger-Tal *et al.* 2010). Therefore, nest abandonment in Tree Sparrows may occur when the cost of re-breeding is lower than that of abandoning the nest. Tree Sparrows generally produce secondary and even tertiary clutches in temperate regions and have a long breeding season from early spring to midsummer (Sasvári & Hegyi 1994, Summers-Smith 1995, Lee *et al.* 2020).

Additionally, since Tree Sparrows are cavity nesters, deformation of the nest entrance may indicate a direct threat regarding potential nest predation. Therefore, when there is a direct predatory threat, breeding Tree Sparrow pairs may consider it more advantageous to attempt to construct a new nest.

The nest surveying method used in the present study was changed after confirming nest abandonment. We began using methods mentioned earlier, such as opening roof tiles from above and using an endoscopic camera to survey the nests while disturbing the breeding pairs as little as possible. Therefore, we strongly suggest taking the utmost care not to alter the size or shape of the nest entrance when surveying Tree Sparrow nests.

*

Acknowledgements – This study was supported by the National Research Foundation of Korea (NRF) grant funded by the Korean government (MSIT) [NRF-2019R1F1A1061024]. We would particularly like to thank Prof. Ji-Woong Lee and Hyun Jeong from the College of Agriculture and Life Sciences of CNU for providing access to the study site.

REFERENCES

Beckmann, C. & Martin, K. (2016): Testing hypotheses about the function of repeated nest abandonment as a life history strategy in a passerine bird. – *Ibis* **158**: 335–342. https://doi.org/10.1111/ibi.12361

Berger-Tal, R., Berger-Tal, O. & Munro, K. (2010): Nest desertion by Grey Fantails during nest building in response to perceived predation risk. – *Journal of Field Ornithology* **81**: 151–154. https://doi.org/10.1111/j.1523–1739.2004.00417.x

Bordjan, D. & Tome, D. (2014): Rain may have more influence than temperature on nest abandonment in the Great Tit Parus major. – *Ardea* **102**: 79–86. https://doi.org/10.5253/078.102.0107

Brunton, D. H. (1997): Impacts of predators: center nests are less successful than edge nests in a large nesting colony of Least Terns. – *The Condor* **99**: 370–380. https://doi.org/10.2307/1369943

Chae, H. (2019): *Are you curious about the sparrow?* – EcoNature foundation, Seoul [in Korean]

Collias, N. E. & Collias, E. C. (1971): Some observations on behavioral energetics in the Village Weaverbird. I. Comparison of colonies from two subspecies in nature. – *The Auk* **88**: 124–133. https://doi.org/10.2307/4083967

Collias, N. E., Victoria, J. K., Coutlee, E. L. & Graham, M. (1971): Some observations on behavioral energetics in the village weaverbird. II. All-day watches in an aviary. – *The Auk* **88**: 134–143. https://doi.org/10.2307/4083968

Cordero, P. (1991): Predation in house sparrow and Tree Sparrow (Passer spp.) nests. Pp. 111–120. *In*: Kavanagh, B. P. & Gorski, W. (eds): *Nestling mortality of granivorous birds due to microorganisms and toxic substances.* – Polish Scientific Publishers, Warsaw.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. (2006): Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. – *Proceedings of the Royal Society B: Biological Sciences* **273**: 701–706. https://doi.org/10.1098/rspb.2005.3373

Flegeltaub, M., Biro, P. & Beckmann, C. (2017): Avian nest abandonment prior to laying – a strategy to minimize predation risk? – *Journal of Ornithology* **158**: 1091–1098. https://doi.org/10.1007/s10336–017–1470–7

García-Navas, V. & Sanz, J. J. (2012): Yearly and seasonal variation of breeding parameters in a declining multi-brooded passerine, the Tree Sparrow. – *Ardea* **100**: 79–88. https://doi.org/10.5253/078.100.0112

Gauthier, M. & Thomas, D. W. (1993): Nest site selection and cost of nest building by Cliff Swallows (Hirundo pyrrhonota). – *Canadian Journal of Zoology* **71**: 1120–1123. https://doi.org/10.1139/z93–152

Isaksson, D., Wallander, J. & Larsson, M. (2007): Managing predation on ground-nesting birds: The effectiveness of nest exclosures. – *Biological Conservation* **136**: 136–142. https://doi.org/10.1016/j.biocon.2006.11.015

Lee, J., Nam, W. & Sung, H. (2020): Breeding ecology of the Eurasian Tree Sparrow Passer montanus living in urban area in South Korea. – *Korean Journal of Ornithology* **27**: 81–89. https://doi.org/10.30980/kjo.2020.12.27.2.81

Li, P. & Martin, T. E. (1991): Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. – *The Auk* **108**: 405–418. https://doi.org/10.1093/auk/108.2.405

Maddox, J. D. & Weatherhead, P. J. (2006): Nests without eggs: Abandonment or cryptic predation? – *The Auk* **123**: 135–140. https://doi.org/10.1093/auk/123.1.135

Martin , T. E. (1992): Breeding productivity considerations: what are the appropriate habitat features for management? Pp. 455–473 *In*: Hagan, III, J. M. & Johnston, D. W. (eds): *Ecology and conservation of Neotropical migrants*. – Smithsonian Institution Press, Washington, D.C.

Martin , T. E. (1993): Nest predation and nest sites. – *BioScience* **43**: 523–532.

Martin , T. E. & Li, P. (1992): Life history traits of open- vs. cavity-nesting birds. – *Ecology* **73**: 579–592. https://doi.org/10.2307/1940764

Metz, K. J. (1991): The enigma of multiple nest building by male Marsh Wrens. – *The Auk* **108**: 170–173. https://doi.org/10.1093/auk/108.1.170

Munro, K. (2007): Breeding behavior and ecology of the Grey Fantail (Rhipidura albiscapa). – *Australian Journal of Zoology* **55**: 257–265. https://doi.org/10.1071/ZO07025
Nelson, S. K. & Hamer, T. E. (1995): Nest success and the effects of predation on Marbled Murrelets. Pp. 89–98. *In:* Ralph, C. J., Hunt, G. L., Jr., Raphael, M., G. & Piatt, J. F. (eds): *Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. – Forest Service, US Department of Agriculture, Albany, CA*
Nilsson, S. G. (1984): The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. – *Ornis Scandinavica* **15**(3): 167–175. https://doi.org/10.2307/3675958
Nolan, Jr. V. (1978): *The ecology and behavior of the prairie warbler, Dendroica discolor*. Ornithological monographs, no. 26. – The American Ornithologists' Union, 593 pp. https://doi.org/10.2307/40166732
Pinowski, J. (1968): Fecundity, mortality, numbers and biomass dynamics of a population of the Tree Sparrow (Passer montanus L.). *Ecologia Polska – Seria A* **16**: 1–58.
Remeš, V., Matysiokova, B. & Cockburn, A. (2012): Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. – *Journal of Avian Biology* **43**: 435–444. https://doi.org/10.1111/j.1600–048X.2012.05599.x
Sasvári, L. & Hegyi, Z. (1994): Colonial and solitary nesting choice as alternative breeding tactics in Tree Sparrow Passer montanus. – *Journal of Animal Ecology* **63**(2): 265–274. https://doi.org/10.2307/5545
Slagsvold, T. (1984): Clutch size variation of birds in relation to nest predation: on the cost of reproduction. – *The Journal of Animal Ecology* **53**: 945–953. https://doi.org/10.2307/4669
Sonerud, G. A. (1985): Nest hole shift in Tengmalm's owl Aegolius funereus as defence against nest predation involving long-term memory in the predator. – *The Journal of Animal Ecology* **54**: 179–192. https://doi.org/10.2307/4629
Stanley, T. R. (2002): How many kilojoules does a Black-billed Magpienest cost? – *Journal of Field Ornithology* **73**: 292–297. https://doi.org/10.1648/0273–8570–73.3.292
Summers-Smith, J. (1995): The Tree Sparrow. – Bath Press, Bath, 206 pp.
Vaske, J. J., Rimmer, D. W. & Deblinger, R. D. (1994): The impact of different predator exclosures on Piping Plover nest abandonment (El impacto de diferentes Barreras para Detener Depredadores en el Abandono de Nidos por individuos de Charadrius melodus). – *Journal of Field Ornithology* **65**: 201–209.
Verboven, N. & Tinbergen, J. M. (2002): Nest desertion: a trade-off between current and future reproduction. – *Animal Behavior* **63**: 951–958. https://doi.org/10.1006/anbe.2001.1971
Wesołowski, T. (2002): Anti-predator adaptations in nesting Marsh Tits Parus palustris: the role of nest-site security. – *Ibis* **144**: 593–601. https://doi.org/10.1046/j.1474–919X.2002.00087.x
Williams, G. C. (1966): Natural selection, the costs of reproduction, and a refinement of Lack's principle. – *The American Naturalis* **100**: 687–690. https://doi.org/10.1086/282461
Yamaguchi, N. & Higuchi, H. (2005): Extremely low nesting success and characteristics of life history traits in an insular population of Parus varius namiyei. – *The Wilson Bulletin* **117**: 189–193. https://doi.org/10.1676/04–081

Revised version submitted December 19, 2022; accepted January 13, 2023; published February 28, 2023