Scerbicke, M. J., J. K. Dodson, P. J.-R. Page, A. R. Hall, and B. D. Peer. 2024. Nest usurpation and adult mortality in a secondary cavity-nesting songbird. Journal of Field Ornithology 95(2):7. https://doi.org/10.5751/JFO-00477-950207

Avian Behavior, Ecology, and Evolution

Nest usurpation and adult mortality in a secondary cavity-nesting songbird

Usurpación de nidos y mortalidad adulta en un ave paseriforme nidificadora secundaria de cavidades

Matthew J. Scerbicke[1], *Jacob K. Dodson*[1], *Patrick J-R Page*, *Alyssa R. Hall*[1] and *Brian D. Peer*[2]

ABSTRACT. Competition for limited nest sites among secondary cavity-nesting bird species is intense and may result in loss of nests, physical conflict, injury, and occasionally death. The Prothonotary Warbler (*Protonotaria citrea*) is a secondary cavity-nesting species that has experienced a 38% population decline over the past five decades. In the northern portion of their range, Prothonotary Warblers are sympatric with two cavity-nesting species known for their nest usurpation behaviors: the House Wren (*Troglodytes aedon*) and Tree Swallow (*Tachycineta bicolor*). From 2017–2023 we monitored Prothonotary Warbler nests. House Wrens destroyed and usurped 38% of Prothonotary Warbler nests, which represented the greatest cause of nest failure, while Tree Swallows usurped only 1.5% of Prothonotary Warbler nests. We also documented two instances of adult Prothonotary Warblers likely killed by Tree Swallows. Interference competition from House Wrens is likely a significant factor limiting Prothonotary Warbler reproductive success where it is sympatric with these nest competitors.

RESUMEN. La competencia por los limitados sitios de nidificación entre aves paseriformes usuarias secundarias de cavidades es intensa y puede resultar en la pérdida de nidos, conflictos físicos, heridas y ocasionalmente muerte. *Protonotaria citrea* es una especie nidificadora secundaria de cavidades que ha experimentado un declive del 38 % en sus poblaciones durante las últimas cinco décadas. En la porción norte de su rango, esta especies es simpátrica con dos especies nidificadoras secundarias de cavidades conocidas por su comportamiento de usurpación de nidos: *Troglodytes aedon* y *Tachycineta bicolor*. Desde 2017 a 2023 monitoreamos nidos de *P. citrea*. Individuos de *T. aedon* destruyeron y usurparon un 38 % de esos nidos, lo cual representó la mayor causa de fracaso de nidos, mientras que *T. bicolor* solo usurpó un 1,5% de los nidos monitoreados. También documentamos dos eventos de adultos de *P. citrea* muertos presumiblemente por *T. bicolor*. La competencia por interferencia de *T. aedon* es probablemente un factor limitante significativo del éxito reproductivo *P. citrea* donde es simpátrica con estos competidores de nidos.

Key Words: *adult mortality; House Wren; interference competition; nest usurpation; Prothonotary Warbler; Protonotaria citrea; Tachycineta bicolor; Tree Swallow; Troglodytes aedon*

INTRODUCTION

Competition for finite resources can occur through exploitation or interference (Dhondt 2012). Exploitation competition arises when species utilize resources thereby reducing their availability for others (Schoener 1983, Freeman et al. 2019), whereas interference competition involves individuals directly preventing rivals from accessing resources through behavioral tactics (Maurer 1984, Lindenmayer et al. 2023). Interference competition is predicted to become more prevalent when resources are abundant, concentrated, and predictable as investment in resource defense is ecologically inexpensive (Maurer 1984). Competition for nest sites among conspecific and heterospecific secondary cavity-nesting birds is a form of interference competition (Rendell and Robertson 1989, Finch 1990). Secondary cavity-nesting species are unable to construct their own cavities and must locate abandoned woodpecker cavities, naturally formed cavities, or artificial nest boxes in order to reproduce. The availability of these nests may be limited (Lack 1954, Newton 1994, Wiebe 2011, Dhondt 2012) and competition for them often leads to the loss of nests, physical conflict, injury, and occasionally death (Gowaty 1984, Merila and Wiggins 1995, Frye and Rogers 2004, Potti et al. 2021).

The Prothonotary Warbler (*Protonotaria citrea*) is the only secondary cavity-nesting warbler in eastern North America and its population has declined by 38% over the past 50 years (Rosenberg et al. 2016), although it has increased in the northern part of the range (Sauer et al. 2021, Fink et al. 2023). Competition between individual Prothonotary Warblers is intense (Walkinshaw 1938, Slevin et al. 2016) and in the northern portion of the breeding range, the Prothonotary Warbler is sympatric with House Wrens (*Troglodytes aedon*), which frequently destroy the nest contents, and in the process, usurp nests of cavity-nesting species including Prothonotary Warblers (Walkinshaw 1938, Brush 1994, Flaspohler 1996). House Wrens do not always usurp the cavity nests in which they have destroyed the contents (Hannon and Cotterill 1998) and they even destroy the contents of open cup-nesting species that they do not compete against for nest sites (Belles-Isles and Picman 1986). Female House Wrens also prefer males that defend more cavities (Eckerle and Thompson 2006) and this likely favors nest takeover by males.

The Prothonotary Warbler is sympatric with Tree Swallows (*Tachycineta bicolor*), which also usurp nests of other cavity-nesting species and are known for their aggressive tactics to secure nest sites (Finch 1990, Rosvall 2008). Much of the breeding ecology of the Tree Swallow is based on its ability to secure nest cavities (Winkler et al. 2020). Tree Swallows prefer to nest near open water with abundant flying insect prey and avoid nesting in wooded areas where House Wrens are often located (Rendell and Robertson 1989). Here, we report high rates of House Wrens usurping Prothonotary Warbler nests and two instances of adult

[1]Western Illinois University, [2]Department of Biological Sciences, Western Illinois University

Prothonotary Warbler deaths attributed to Tree Swallows, underscoring the significance of interspecific interference competition in shaping the dynamics of these cavity-nesting bird species.

METHODS

This study was conducted at the Princeton Wildlife Management Area just north of Princeton, Iowa (41°72′46″ N, 90°34′59″ W). We also report limited data from the John Deere T. P. C. Golf Course in Coal Valley, IL (41°28′48″ N, 90°23′24″ W). The Princeton Wildlife Management Area is located in the floodplain of the Mississippi and Wapsipinicon Rivers, while the John Deere T. P. C. Golf Course is situated along the Rock River floodplain. We have installed more than 300 nest boxes for Prothonotary Warblers, constructed from either wood or PVC, and they are mounted on electrical conduit poles. Our two most common boxes are standard wooden boxes and PVC boxes with circular entrances with diameters of 45mm. We also used a small number of slot boxes ($n < 30$) designed for Carolina Wrens (*Thryothorus ludovicianus*). Instead of having a circular entrance, the top half of the front of slot boxes are open. Most nest boxes were placed above the water where Prothonotary Warblers prefer to nest (Petit 1999) and some boxes were located parallel to the banks of deeper bodies of water. During drought, boxes occasionally became exposed over dry ground as the season progressed but Prothonotary Warblers still used these boxes (Mueller et al. 2019). Our nest boxes were also used by other secondary cavity-nesting species, primarily House Wrens and Tree Swallows, and occasionally Eastern Bluebirds (*Sialia sialis*). Tree Swallows typically arrive at our sites in the latter half of April, followed by the House Wrens, and then Prothonotary Warblers by the first week of May.

We report results from 2017–2018 and 2020–2023 at the Princeton Wildlife Management Area and from 2018 at one nest at the John Deere T. P. C. Golf Course. The sites were inaccessible for most of 2019 due to flooding of the Mississippi River. We began monitoring nests the first week of May when the Prothonotary Warblers arrived and stopped at the end of the breeding season in mid-July. Nests were checked every 1–3 days. We also recorded interactions continuously with cameras mounted inside of nest boxes (PNZEO miniature video cameras powered by 26800mAh battery packs Ravpower, RP-PB41) from 2020–2023 and cameras located outside of nest boxes (Sony Handycam models HDR-CX190, HDR-CX110; SEREE camcorder 18x optical zoom) that recorded for shorter durations.

We considered nests as usurped if they initially contained nest materials, eggs, or nestlings of one species that were subsequently removed and replaced with the nest of another species. House Wrens punctured eggs and dropped them below nests (Fig. 1), left them in nests (Fig. 2), removed nestlings from nests and dropped them to the ground or into the water (Fig. 3), or failed to remove them completely from a nest and the nestling was left hanging in the entrance (Figs. 4, 5, 6). Tree Swallows only usurped nests and to our knowledge, never destroyed eggs without subsequently taking over the nests. We confirmed these behaviors from video recorded at nests (Videos 1, 2 [https://zenodo.org/records/11127398, https://zenodo.org/records/11127521]). We combined observations of nest destruction and nest usurpation by competitors and categorized them as "destroyed nests" (Table 1). Videos were also monitored for evidence of egg destruction by Brown-headed Cowbirds (*Molothrus ater*).

Fig. 1. Punctured Prothonotary Warbler (*Protonotaria citrea*) egg below the nest.

Fig. 2. Punctured Prothonotary Warbler (*Protonotaria citrea*) eggs inside the nest.

Fig. 3. Prothonotary Warbler (*Protonotaria citrea*) eggs and nestling below the nest.

Fig. 4. Dead Brown-headed Cowbird (*Molothrus ater*) nestling hanging in the nest entrance.

Fig. 5. Dead Prothonotary Warbler (*Protonotaria citrea*) nestling hanging outside the nest entrance.

Fig. 6. The same dead Prothonotary Warbler (*Protonotaria citrea*) nestling hanging inside the nest entrance along with two living warbler nestlings.

Table 1. Number of nests initiated by Prothonotary Warblers (*Protonotaria citrea*), House Wrens (*Troglodytes aedon*), and Tree Swallows (*Tachycineta bicolor*) at our study site in Scott County, IA, and nest destruction and nest usurpation rates.

Species	Number of nests initiated	Percentage of nests destroyed/ usurped
Prothonotary Warbler	534	38.4% by House Wrens 1.5% by Tree Swallows
House Wren	334	0.3% by Tree Swallows 0% by Prothonotary Warblers
Tree Swallow	60	1.7% by House Wrens 0% by Prothonotary Warblers

RESULTS

Nest usurpation rate

A total of 38.4% of 534 Prothonotary Warbler nests were usurped or destroyed by House Wrens and 1.5% of nests were usurped by Tree Swallows at Princeton Wildlife Management Area (Table 1). There was no significant annual variation in usurpation rates (2017: 52/86 nests; 2018: 34/79 nests; 2020: 54/89 nests; 2021: 16/86 nests; 2022: 15/97 nests; 2023: 34/97 nests; one-way ANOVA, $F_{1,4} = 1.89$, $P = 0.24$). House Wrens and Tree Swallows only usurped one nest each from one another, and Prothonotary Warblers never usurped nests from House Wrens or Tree Swallows (Table 1).

Adult mortality

On 14 May 2018, a nest was found at the John Deere T. P. C. Golf Course with two adult Tree Swallows perched on top of the box and a deceased male Prothonotary Warbler inside the box (Fig. 7). There was a small amount of moss inside the box. The bird was removed and there were matted feathers around its head and neck. The Tree Swallows subsequently completed a nest and laid eggs in this box.

Fig. 7. Adult male Prothonotary Warbler (*Protonotaria citrea*) found dead inside the nest box defended by Tree Swallows (*Tachycineta bicolor*).

On 29 May 2023, while approaching a nest box at the Princeton Wildlife Management Area, one of us (MJS) was attacked by a pair of Tree Swallows. The box contained a feather-lined Tree Swallow nest with six eggs. A dead female Prothonotary Warbler was suspended from a gap where the door of the box typically closes (Fig. 8). Nest material surrounded both the Prothonotary Warbler's legs. A superficial inspection revealed no obvious signs of trauma on the bird.

Fig. 8. A dead female Prothonotary Warbler (*Protonotaria citrea*) hanging from the nest box following usurpation by Tree Swallows (*Tachycineta bicolor*).

DISCUSSION

Nest usurpation

House Wrens were much more likely to destroy and usurp Prothonotary Warbler nests compared to Tree Swallows. House Wrens destroyed or usurped 38.4% of Prothonotary Warbler nests and Tree Swallows took over only 1.5% of nests. We never recorded Tree Swallows destroying the contents of any nests, whether it be those of Prothonotary Warblers or House Wrens. This may be due in part to Tree Swallows being relatively rare at our site compared to the House Wrens and Prothonotary Warblers (Table 1). Similar to other studies, House Wrens did not always usurp nests after they destroyed the contents and this is thought to eliminate competition (Belles-Isles and Picman 1986, Finch 1990, Pribil and Picman 1991, Kattan 2016). We also found that House Wrens occasionally consumed eggs and this is the first evidence of them doing so to our knowledge (Video 2, https://zenodo.org/records/11127521). Prothonotary Warblers were

never observed usurping nests from either one of these competitors, although they do occasionally maintain control of nest boxes after partial clutch reduction from House Wrens (Video 3, https://zenodo.org/records/11127535). Thus, Prothonotary Warblers appear to be less likely to usurp nests from these two competitors and are especially vulnerable to having their nests usurped.

Our estimates of nest destruction by House Wrens are likely conservative because there were instances in which eggs disappeared with no obvious signs of wren activity. Some of these additional cases of nest failure could have been due to predators such as fox snakes (*Pantherophis ramspotti*) or raccoons (*Procyon lotor*), but damage from raccoons is obvious because of the disturbance inside and around the nest, and snakes are rare at our study site (personal observation). Moreover, we have recorded >5000 hours of video at Prothonotary Warbler nests both day and night, and have never recorded predation by mammals or snakes; the only species we have recorded on video destroying eggs or nestlings is the House Wren (n = 37). Brown-headed Cowbirds parasitize Prothonotary Warbler nests at a high rate at our study sites (62%; in review) and are known to sometimes destroy nest contents when they discover nests that are too advanced in the nest cycle to be parasitized (i.e., "farming"; Peer 2006, Hoover and Robinson 2007), however, our videos did not reveal any instances of this behavior (unpublished data). We have recorded >100 Brown-headed Cowbirds laying in Prothonotary Warbler nests before dawn and >200 Brown-headed Cowbird prospecting visits after dawn, and none of these involved farming behavior (unpublished data). We did observe one female Brown-headed Cowbird removing eggs from a House Wren nest (in review), which are rarely used hosts (Pribil and Picman 1997). Destruction of host eggs by Brown-headed Cowbirds varies (e.g., Arcese et al. 1996, McLaren and Sealy 2001) and it appears to be rare at our site.

Other studies of Prothonotary Warbler populations sympatric with House Wrens have reported results similar to our findings. Walkinshaw (1941) found that the nest success of Prothonotary Warblers was twice as high in Tennessee compared to Michigan and implicated House Wrens in the majority of nest losses in the Michigan population. Over the course of seven years in Ontario, House Wrens were responsible for the majority of nest failures (Dobbyn and McCracken 2005; McCracken and Wood 2005, unpublished data). Brush (1994) studied Prothonotary Warblers at one of our sites (Princeton Wildlife Management Area) and reported that House Wrens were also the primary cause of nest failure. House Wrens are responsible for the majority of nest losses in other secondary cavity-nesting species including the Carolina Chickadee (*Poecile carolinensis*; Doherty and Grubb 2002), Black-capped Chickadee (*P. atricapillus*; Kluyver 1961, Brewer 1963), Tree Swallow (Finch 1990), Eastern Bluebird (Tuttle 1991), and have been linked with the decline of the Bewick's Wren (*Thryomanes bewickii*; Kennedy and White 1996). The Prothonotary Warbler was recently listed as a Species of Continental Concern due to a 38% decline over the past 50 years (Rosenberg et al. 2016) and while House Wrens appear to be the most frequent cause of nest failure in our study area, Prothonotary Warbler populations in general are increasing in the northern portion of the range where they are sympatric with House Wrens (Sauer et al. 2021, Fink et al. 2023). It is possible that the interspecific interference competition we and others have documented is more intense than what occurs in natural cavities because the birds may prefer the artificial nest boxes that are relatively safe from terrestrial predators. Other studies have shown that secondary cavity-nesters prefer nest boxes over natural cavities (Drilling and Thompson 1988) and relatively few Prothonotary Warblers or House Wrens nested in natural cavities at our site (unpubl. data). Because the majority of research on these birds is conducted using artificial nest boxes, research is needed on nest usurpation patterns within natural cavities to determine if Prothonotary Warblers have higher nest success in natural cavities where they are sympatric with House Wrens.

Adult warbler mortality

We found two dead adult Prothonotary Warblers inside nest boxes occupied by Tree Swallows. The male Prothonotary Warbler was found lifeless inside the nest box with some moss, which indicates it was likely in the early stages of settling into this nest because males add moss first and then sing to attract females who then complete the nest (Petit 1999). The female Prothonotary Warbler was found suspended from the gap at the bottom of the box where the door closes. The nail which typically secures the door of the nest box apparently became dislodged during the flood of 2023 and we were unable to access the site until the flood waters receded in mid-May. Whether the female attempted to escape through that gap or whether the Tree Swallows forced her body through the gap after possibly killing her and subsequently building the nest is unknown.

We cannot be certain that swallows were responsible for these deaths and it is possible that the birds died from other causes (e.g., Petit and Petit 1987). However, we can rule out predation because the birds would have been consumed if predators were responsible. The Prothonotary Warbler that was examined closely had evidence of trauma around the head and neck, which is similar to the injuries observed by Robertson et al. (1986) after observing Tree Swallows fighting and dead inside of nest boxes. Moreover, in seven years of studying this system and having checked >1000 nest boxes, we have only observed two dead adult birds inside boxes and both were Prothonotary Warblers in nests occupied by Tree Swallows. Our observations are similar to Rogers et al. (2020) who observed dead Prothonotary Warblers incorporated in two Tree Swallow nests and they likewise attributed the deaths to Tree Swallows. Other studies have found evidence that male and female Tree Swallows commit infanticide (Chek and Robertson 1991), kill adult conspecifics inside of nest boxes (Lombardo 1986, Robertson et al. 1986), and kill other cavity-nesting species inside of boxes (Kuerzi 1941). Therefore, our inference is not without precedent.

Tree Swallows are more likely than House Wrens to kill competitors. There are only three recorded instances of House Wrens killing heterospecific competitors and two cases where conspecifics were killed. Kendeigh (1941) found two adult Eastern Bluebirds dead inside nest boxes and concluded House Wrens were likely responsible, and Beckwith (1913) witnessed a wren killing a House Sparrow (*Passer domesticus*). Belles-Isles and Picman (1987) found two dead male House Wrens inside boxes being defended by other male House Wrens.

CONCLUSION

While the majority of the Prothonotary Warbler breeding population occurs south of the geographic range of the House Wren, interference competition with House Wrens has a substantial influence on Prothonotary Warbler reproductive success in the

northern portion of their range and offers insight into the complexities of interspecific interactions when species compete for limited resources. These observations contribute to our understanding of the dynamics between these species in shared habitats. This research highlights the importance of continued vigilance in examining evolving species interactions and the broader ecological context of avian communities.

Acknowledgments:

The Iowa D. N. R., Iowa Ornithological Society, Iowa Audubon Society, Quad City Audubon, Western Prairie Audubon, and Western Illinois University provided funds for this research. We thank the Subject Editor and two anonymous reviewers who provided helpful comments that improved the manuscript.

Data Availability:

Data are available upon request.

LITERATURE CITED

Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences 93 (10):4608-4611. https://doi.org/10.1073/pnas.93.10.4608

Beckwith, R. 1913. Our friend, the House Wren. Bird-Lore 15:244-245.

Belles-Isles, J. C., and J. Picman. 1986. House Wren nest-destroying behavior. Condor 88(2):190-193. https://doi.org/10.2307/1368914

Belles-Isles, J. C., and J. Picman. 1987. Suspected adult intraspecific killing by House Wrens. Wilson Bulletin 99:497-498.

Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. Auk 80(1):9-47. https://doi.org/10.2307/4082581

Brush, T. 1994. Effects of competition and predation on Prothonotary Warblers and House Wrens nesting in eastern Iowa. Iowa Academy of Science 101:28-30.

Chek, A. A., and R. J. Robertson. 1991. Infanticide in female Tree Swallows: a role for sexual selection. Condor 93(2):454-457. https://doi.org/10.2307/1368967

Dhondt, A. A. 2012. Interspecific competition in birds. Oxford University Press, Oxford, England.

Dobbyn, S., and J. McCracken. 2005. The causes and effects of interspecific competition by House Wrens (Troglodytes aedon) on the recovery of the Prothonotary Warbler (Protonotaria citrea) in Rondeau Provincial Park. Pages 347-359 in G. Nelson, T. Nudds, M. Beveridge, B. Dempster, L. Lefler, and E. Zajc, editors. Proceedings of the Parks Research Forum of Ontario: Protected Areas and Species and Ecosystems at Risk - Research and Planning Challenges; 5-7 May 2005. University of Guelph, Ontario, Canada.

Doherty Jr., P. F., and T. C. Grubb Jr. 2002. Nest usurpation is an "edge effect" for Carolina Chickadees Poecile carolinensis. Journal of Avian Biology 33:77-82. https://doi.org/10.1034/j.1600-048X.2002.330112.x

Drilling, N. E., and C. F. Thompson. 1988. Natal and breeding dispersal in House Wrens (Troglodytes aedon). Auk 105 (1):480-491. https://doi.org/10.1093/auk/105.3.480

Eckerle, K. P., and C. F. Thompson. 2006. Mate choice in House Wrens: nest cavities trump male characteristics. Behaviour 143:253-271. https://doi.org/10.1163/156853906775900694

Finch, D. M. 1990. Effects of predation and competitor interference on nesting success of House Wrens and Tree Swallows. Condor 92(3):674-687. https://doi.org/10.2307/1368686

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, C. Crowley, K. Dunham, A. Stillman, I. Davies, A. Rodewald, V. Ruiz-Gutierrez, C. Wood. 2023. eBird Status and Trends, Data Version: 2022; Released: 2023. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/ebirdst.2022

Flaspohler, D. J. 1996. Nesting success of the Prothonotary Warbler in the upper Mississippi River bottomlands. Wilson Bulletin 108:457-466.

Freeman, B. G., J. A. Tobias, and D. Schluter. 2019. Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds. Ecography 42 (11):1832-1840. https://doi.org/10.1111/ecog.04606

Frye, G. G., and K. K. Rogers. 2004. Probable cavity usurpation via interspecific killing by the Mountain Bluebird (Sialia currucoides). Northwestern Naturalist 85(3):126-128. https://doi.org/10.1898/1051-1733(2005)085[0126:PCUVIK]2.0.CO;2

Gowaty, P. A., and A. A. Karlin. 1984. Multiple maternity and paternity in single broods of apparently monogamous Eastern Bluebirds (Sialia sialis). Behavioral Ecology and Sociobiology 15:91-95. https://doi.org/10.1007/BF00299374

Hannon, S. J., and S. E. Cotterill. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. Auk 115(1):16-25. https://doi.org/10.2307/4089107

Hoover, J. P., and S. K. Robinson. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. Proceedings of the National Academy of Sciences 104 (11):4479-4483. https://doi.org/10.1073/pnas.0609710104

Kattan, G. H. 2016. Heterospecific infanticidal behavior by southern House Wrens (Troglodytes aedon musculus) suggests nest site competition. Wilson Journal of Ornithology 128 (4):899-903. https://doi.org/10.1676/15-129.1

Kennedy, E. D., and D. W. White. 1996. Interference competition from House Wrens as a factor in the decline of Bewick's Wrens. Conservation Biology 10(1):281-284. https://doi.org/10.1046/j.1523-1739.1996.10010281.x

Kendeigh, S. C. 1941. Territorial and mating behavior of the House Wren. Illinois Biological Monographs 18(3):1-120. https://doi.org/10.5962/bhl.title.50316

Kluyver, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. Auk 78(4):532-550. https://doi.org/10.2307/4082187

Kuerzi, R. G. 1941. Life history studies of the Tree Swallow. Proceedings of the Linnean Society New York 52-53:1-52.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford, UK.

Lindenmayer, D. B., W. Blanchard, M. J. Evans, R. Beggs, T. Lavery, D. Florance, C. Crane, D. Smith, A. Siegrist, E. Lang, and B. C. Scheele. 2023. Context dependency in interference competition among birds in an endangered woodland ecosystem. Diversity and Distributions 29(4):556-571. https://doi.org/10.1111/ddi.13680

Lombardo, M. P. 1986. A possible case of adult intraspecific killing in the Tree Swallow. Condor 88(1):112. https://doi.org/10.2307/1367772

Maurer, B. A. 1984. Interference and exploitation in bird communities. Wilson Bulletin 96:380-395.

Merila, J., and D. J. Wiggins. 1995. Interspecific competition for nest holes causes adult mortality in the Collared Flycatcher. Condor 97(2):445-450. https://doi.org/10.2307/1369030

Mueller, A. J., D. J. Twedt, and E. K. Bowers. 2019. Rapid adoption of nest boxes by Prothonotary Warblers (Protonotaria citrea) in mesic deciduous forest. Canadian Journal of Zoology 97(12):1109-1115. https://doi.org/10.1139/cjz-2019-0059

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70 (3):265-276. https://doi.org/10.1016/0006-3207(94)90172-4

Peer, B. D. 2006. Egg destruction and egg removal by avian brood parasites: adaptiveness and consequences. Auk 123(1):16-22. https://doi.org/10.1093/auk/123.1.16

Petit, L. J., and D. R. Petit. 1987. Non-violent deaths of female Prothonotary Warblers on their nests. Journal of Field Ornithology 58:52-54.

Petit, L. J. 1999. Prothonotary Warbler (Protonotaria citrea) in A. F. Poole and F. B. Gill, editors. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.prowar.02

Potti, J., C. Camacho. D. Canal, and J. Martínez-Padilla. 2021. Three decades of crimes and misdemeanours in the nest box life of European Pied Flycatchers Ficedula hypoleuca. Ardeola 68 (2):315-333. https://doi.org/10.13157/arla.68.2.2021.ra1

Pribil, S., and J. Picman. 1991. Why House Wrens destroy clutches of other birds: a support for the nest site competition hypothesis. Condor 93(1):184-185. https://doi.org/10.2307/1368624

Pribil, S., and J. Picman. 1997. Parasitism of House Wren nests by Brown-headed Cowbirds: why is it so rare? Canadian Journal of Zoology 75(2):302-307. https://doi.org/10.1139/z97-038

Rendell, W. B., and R. J. Robertson. 1989. Nest site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. Condor 91(4):875-885. https://doi.org/10.2307/1368072

Robertson, R. J., H. L. Gibbs, and B. J. Stutchbury. 1986. Spitefulness, altruism, and the cost of aggression: evidence against superterritoriality in Tree Swallows. Condor 88 (1):104-105. https://doi.org/10.2307/1367767

Rogers, S. L., T. N. Parlow, J. Kacmarcik, R. Reilly, C. Viverette, and L. P. Bulluck. 2020. Prothonotary Warbler nestlings fledge from mixed broods following nest takeovers by Tree Swallows. Northeastern Naturalist 27(4):N63-N70. https://doi.org/10.1656/045.027.0414

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, A. Couturier, D. W. Demarest, W. E. Easton, J. J. Giocomo, R. H. Keller, A. E. Mini, A. O. Panjabi, D. N. Pashley, T. D. Rich, J. M. Ruth, H. Stabins, J. Stanton, and T. Will. 2016. Partners in flight landbird conservation plan: 2016 revision for Canada and continental United States. Partners in Flight Science Committee.

Rosvall, K. A. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with Tree Swallows. Animal Behaviour 75(5):1603-1610. https://doi.org/10.1016/j.anbehav.2007.09.038

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2021. The North American Breeding Bird Survey, Results and Analysis 1966 - 2021. Version 2.07.2021. United States Geological Survey.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122(2):240-85. https://doi.org/10.1086/284133

Slevin, M. C., D. W. Raybuck, and T. J. Boves. 2016. Prothonotary Warblers (Protonotaria citrea) break their beaks during attacks on wooden conspecific decoys. Wilson Journal of Ornithology 128(1):193-197. https://doi.org/10.1676/1559-4491-128.1.193

Tuttle, R. M. 1991. An analysis of the interspecific competition of Eastern Bluebirds, Tree Swallows, and House Wrens in Delaware State Park, Delaware, Ohio, 1979-1986. Sialia 13:3-13.

Walkinshaw, L. H. 1938. Nesting studies of the Prothonotary Warbler. Bird-Banding 9(1):32-46. https://doi.org/10.2307/4509491

Walkinshaw, L. H. 1941. The Prothonotary Warbler, a comparison of nesting conditions in Tennessee and Michigan. Wilson Bulletin 53:3-21.

Wiebe, K. L. 2011. Nest sites as limiting resources for cavity-nesting birds in mature forest ecosystems: a review of the evidence. Journal of Field Ornithology 82(3):239–248. https://doi.org/10.1111/j.1557-9263.2011.00327.x

Winkler, D. W., K. K. Hallinger, D. R. Ardia, R. J. Robertson, B. J. Stutchbury, and R. R.Cohen. 2020. Tree Swallow (Tachycineta bicolor) in A. F. Poole, editor. Birds of the world online. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.treswa.01