



Avian Behavior, Ecology, and Evolution

Observations of the territorial behavior of the Prothonotary Warbler: male within- and between-season relocations, polyterritoriality, and the role of extraterritorial explorations

Observaciones del comportamiento territorial de la Reinita Protonotaria: relocalizaciones de los machos durante y entre las temporadas, politerritorialidad, y el papel de exploraciones extraterritoriales

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ABSTRACT. From 1983 to 1987, a natural riverine population, without the use of artificial nest boxes, of Prothonotary Warblers (*Protonotaria citrea*) was studied along a 10.5 km section of the North Fork of Salt Creek, located in Monroe County, Indiana, USA. During the study, 101 territorial males were captured and marked, and their subsequent movements documented. Of these, 31 (31%) returned to the study area in at least one subsequent year, and these resulted in 21 cases of males returning to the territory of the previous year and 13 observations of males returning to a different territory from that of the previous year. Eleven males were observed to relocate their territories within-season. Nine of these were individuals unable to attract a female to the initial site, with this pattern being statistically significant. Two cases of polyterritorial polygyny were observed, representing the first documentation of this behavior in the Prothonotary Warbler. No evidence was found suggesting the presence of a population of “floaters”: nonterritorial males unable to find suitable nesting territories. By mid-May of the 1984 to 1986 seasons, all territorial males had been captured and marked with all subsequent observations each year being of known individuals. In addition, during all years of the study, apparently suitable Prothonotary Warbler habitat along the stream was unoccupied by territorial males. Long distance homing to the breeding territory by a male, captured and released 47 km from the initial site is reported. Male extraterritorial exploration forays were observed, with detailed observations being made of eight individuals observed wandering a large distance from their respective territories. Some males were observed more than once, resulting in 11 observations of exploration. The results of this study suggests that male exploring behavior in the Prothonotary Warbler plays a role in a general dispersal mechanism in this species.

RESUMEN. De 1983 a 1987, se estudió una población ribereña natural de Reinita Protonotaria (*Protonotaria citrea*), sin el uso de nidos artificiales, a lo largo de un tramo de 10,5 km del North Fork de Salt Creek, ubicado en el condado de Monroe, Indiana, Estados Unidos. Durante el estudio, se capturaron y se marcaron 101 machos territoriales y se documentaron sus movimientos posteriores. De estos, 31 (31%) regresaron al área de estudio en al menos un año más tarde, resultando en 21 casos de machos que regresaron al territorio del año anterior y 13 observaciones de machos que regresaron a un territorio diferente al del año anterior. Se observó que once machos reubicaban sus territorios dentro de la temporada. Nueve de ellos eran individuos incapaces de atraer a una hembra al sitio inicial, siendo este patrón estadísticamente significativo. Se observaron dos casos de poligamia politerritorial, lo que representa la primera documentación de este comportamiento en la Reinita Protonotaria. No se encontró evidencia que sugiriera la presencia de una población de “voladores flotantes”: los machos no territoriales no pueden encontrar territorios adecuados para anidar. A mediados de mayo en las temporadas de 1984 a 1986, todos los machos territoriales habían sido capturados y marcados y todas las observaciones posteriores de cada año correspondieron a individuos conocidos. Además, durante todos los años del estudio, el hábitat aparentemente adecuado para la Reinita Protonotaria a lo largo del arroyo estuvo desocupado por machos territoriales. Se reporta el regreso a larga distancia al territorio de reproducción por parte de un macho, capturado y liberado a 47 km del sitio inicial. Se observaron incursiones de exploración extraterritorial de machos, y se realizaron observaciones detalladas de ocho individuos que deambulaban a gran distancia de sus respectivos territorios. Algunos machos fueron observados más de una vez, lo que resultó en 11 observaciones de exploración. Los resultados de este estudio sugieren que el comportamiento de exploración del macho en la Reinita Protonotaria juega un papel en un mecanismo de dispersión general en esta especie.

Key Words: *Extraterritorial exploration; polyterritorial polygyny; Prothonotary Warbler; territory relocation*

INTRODUCTION

Based upon the long history of researchers concentrating on the nesting behavior of North American New World Warblers (Parulidae; e.g., Bent 1953), these birds have been assumed to be all socially monogamous with biparental care of nestlings being the rule (Winkler et al. 2020). Over time, evidence has accumulated suggesting that warbler breeding systems are more complex than previously thought, with the presence of “floaters,” non-territorial individuals precluded from breeding because of the lack of available habitat, and wandering territorial males searching for better locations (Morse 1989). Identification of such

individuals requires a well-marked population and a large study area, which is not often the case in many studies.

The Prothonotary Warbler (*Protonotaria citrea*) is an ideal species in which to study territorial behavior in a parulid. The species has, in the majority of cases, very specific habitat requirements, consisting of flooded areas with the presence of available nesting cavities (Bent 1953). Males are easily captured on their territory with song playback, allowing the marking of all males in an area, and females can be efficiently captured while incubating or brooding at the nest cavity.

From 1983 to 1987, a riverine population of Prothonotary Warblers was studied along the North Fork of Salt Creek, located in eastern Monroe Co., Indiana, USA. During the 1983 to 1986 seasons, by mid-May, all territorial males in the area were captured and marked, along with a smaller sample of females and young of the year. The “beads on a string” nature of the placement of territories along the stream (Fig. 1) allowed the relatively easy documentation of male within- and between- season movements of marked individuals. This study documents the territorial behavior of male Prothonotary Warblers in a natural situation without the use of nest boxes. Details of within- and between-season male territorial movements are reported, as well as observations of male extraterritorial explorations. In addition, the first observations of polyterritorial polygyny in the Prothonotary Warbler are described.

Fig. 1. Pooled 1984 and 1985 territories. Some sites were occupied both years.



METHODS

The study area, along the North Fork of Salt Creek, was located 5 km east of Bloomington, Indiana, USA (39°04'14"N 86°23'50" W), with the stream feeding into Monroe Reservoir to the south. The study area encompassed a straight north to south distance of 4.9 km and a stream distance of 10.5 km. In 1983, fieldwork was confined to the upper third of the stream, a total of 3.8 km stream distance. This was extended in 1984 to 1987 to the full length of 10.5 km stream distance to the point where the North Fork of Salt Creek enters Monroe Reservoir. The width of the stream varied from approximately 10 m in the upper third to 30 m in the lower third. During the study, Prothonotary Warblers spent most of their time along the North Fork of Salt Creek and were rarely observed more than 30 m inland from the stream.

Using the average stream width of 20 m and 30 m on both sides of the stream gives a rough estimate of 84 ha of Prothonotary Warbler habitat on the study area.

The Prothonotary Warbler is unique among eastern North American Warblers in that it is a cavity nester. Common nest locations are old Downy Woodpecker (*Dryobates pubescens*) nests, as well as in other cavities in dead stumps (Bent 1953), and this was the case on the North Fork of Salt Creek study site. Nests are mostly placed over or within 5 m of standing water, with a mean height of 2 m and a range of 0.5 m to 10 m (Walkinshaw 1953). The species also readily accepts nest boxes (Blem and Blem 1991). No nest boxes were used during this study.

Male Prothonotary Warblers were captured on their territory by use of conspecific song playback and a male stuffed decoy. Females were captured while incubating or brooding by placing a mist net over the cavity entrance and then flushing the female into the net. When a nest was accessible, nestlings were banded around day 8 of the nestling period. All individuals captured were color banded. Weights and measurements of these has been previously reported (Kowalski 1986).

From 1983 to 1986, the study area was visited daily from 24 April to 31 August. Once the study area was extended in 1984, the area was covered in three sections, with each section covered on alternative days. On these days, the section was examined for the presence of male warblers and each known territory was visited. If unmarked territorial males were found, the individuals were captured and banded using one metal band and up to three color bands. From 1983 to 1986, all territorial males on the study area were color-banded by mid-May. Coverage of each section required a minimum of 4 h to complete. In 1987, only four visits to the study area were made, between 29 April and 12 June, with the sole purpose of locating any returning banded warblers from previous years.

To test the possibility of homing to the breeding territory, on 9 June 1985 four unmated territorial males were captured using song playback and transported in opaque paper bags and released at a site on the West Fork of the White River, Morgan Co., Indiana, USA. The release site was located 47 km due north of the North Fork of Salt Creek study area and in a separate drainage.

ANALYSIS

Taking into account the paucity of observations in 1987, the calculation of observed adult male survivorship does not include individuals first banded in 1986 nor does it include four unmated males who were removed from their respective territories in 1985 as part of a homing experiment. Most observed movements of male Prothonotary Warblers were along the banks of the North Fork of Salt Creek. However, on occasion, individuals would cut across sections of forest to reach another part of the stream. Taking this into account, movements are reported as the straight-line distance (minimum), stream distance (maximum), and mean distance.

The most intense field work was done during the 1984 and 1985 seasons, where all male Prothonotary Warbler territories along the North Fork of Salt Creek were mapped. Figure 1 shows the pooled locations of 1984 and 1985 male territories.

RESULTS

Adult male survivorship

Based upon banded male returns to the study site, assuming no dispersal from the study area, observed adult male survivorship was 31% (Table 1). This is similar to the 27% reported by Wood and Reasor (2006) and the 24% reported by Walkinshaw (1953).

Table 1. Observed survivorship of male Prothonotary Warblers (*Protonotaria citrea*). Recovery years are entered as the number of males returning/maximum possible number of males by year.

Males banded by year (N = 101)	1984	1985	1986	Total
1983 (N = 7)	4/7	2/4	0/2	
1984 (N = 49)		19/49	2/19	
1985 (N = 45)			12/45	
N	4/7	21/53	14/66	39/126
%	57	40	21	31

Male territorial behavior

Males not returning to the study area

Between 1983 and 1986, a total of 101 territorial males were captured and color-banded by use of song playback and a stuffed mount. During all years of the study, 67 (66%), were never observed again after the initial capture as territorial individuals. The lack of subsequent observations of these males was most likely the result of relocation off of the study site. It is possible that these birds were floaters (Winker 1998). However, no evidence of the existence of floaters on the North Fork of Salt Creek area was found. This is discussed in more detail in the section on male exploration behavior below and in the discussion.

Site fidelity

Of the 101 territorial males banded, 31 (31%) returned to the study area in at least one subsequent year. From this group of 31 males, 21 (68%) returned to the territory of the previous year.

Between-year territory relocations

A total of 13 returning males were found to return to different territories from the previous year. Two of these males relocated in more than one year, giving a total of 15 relocation histories. Table 2 gives the distances of the between-year territory relocations.

Table 2. Between-year male territorial relocation distances.

N = 15	Straight distance (m)	Stream distance (m)	Mean distance (m)
Minimum	214	214	214
Maximum	2000	3262	2500
Mean	816	1095	952
Standard error	154	241	195
Median	556	704	630

Within-year territory relocations

Eleven territorial males were captured by use of song playback with a stuffed mount and subsequently relocated their territories in that year (Table 3). Of these, nine relocated to a site downstream

from the initial territory, a preference that was significant ($X^2 = 4.45$, $df = 1$, $p = 0.03$), assuming an equal probability of an individual moving up or downstream. An exception to this was male #31/1985. This male initially took a territory on 23 April 1985, near the southern (downstream) edge of the study area and was unable to attract a female. He was not observed again on that territory. On 5 June 1985, this male was recaptured with song playback at an upstream distance (straight line distance, stream distance, mean distance) of 4481 m, 9000 m, and 6741 m, respectively, where he successfully obtained a mate and fledged young. The distance of this male's relocation from the initial capture site supports the notion that many of the males captured once and never seen again (see above) had simply relocated off of the study area.

Table 3. Within-year male territorial relocation distances.

N = 11	Straight distance (m)	Stream distance (m)	Mean distance (m)
Minimum	185	185	185
Maximum	4481	9000	6741
Mean	999	1738	1372
Standard error	357	746	551
Median	481	778	630

Of the 11 within-year relocating males, nine were not able to attract a female to the first territory, a trend that was significant ($X^2 = 4.45$, $df = 1$, $p = 0.03$) assuming an equal probability of mated and unmated males relocating. This contrasts with the case of within-year relocating Prairie Warblers (*Setophaga discolor*), where Nolan (1978) found that relocation was not associated with the inability to acquire a female on the initial territory. In the group of nine initially unmated males, four remained unmated on the relocated territory while five successfully mated and nested on the relocated site.

Two males were observed with females on the initial territory. It was not directly observed whether or not these males successfully bred on the first territory. One of these, male #18/1985, was found on the relocated territory feeding fledglings on 8 June 1985, 41 days after the initial capture on 29 April 1985 on the first territory. Given that the approximate time from nest building to fledging for Prothonotary Warblers is 31 days (Petit 2020) it is unlikely that this male successfully bred on the first territory. The second male, #30/1985, was captured on the initial territory on 20 April 1985 and was recaptured on the relocated site with a different female and a nest 42 days later, suggesting the possibility that this male may have successfully bred on the first site.

The details of male Prothonotary Warbler within-year relocation distances are given in Table 3. The only relocation distance data available in the literature for a parulid is the straight-line distances for male Prairie Warbler relocations (Nolan 1978:32). Mean straight line relocation distances for Prothonotary Warblers in this study (999 m) did not significantly differ from that of Nolan's Prairie Warblers (711 m; $t = 0.611$, $p = 0.55$). Nor did the median distance for Prothonotary Warbler relocations (556 m) and Prairie Warblers (293 m) significantly differ (Mood's median test: $X^2 = 2.11$, $df = 1$, $p = 0.15$; Zar 1974). Of the 11 males who relocated within-season, five (45%) subsequently returned to the study area. Of these five, three (60%) returned to the relocated territory of

the previous year. One male relocated the second year to a territory equidistant between the initial and relocated territories of the previous year.

One male, #32/1985, relocated territories in 1985 and in 1986 returned to the initial territory of 1985. In 1987, this individual returned and mated on the relocated territory of 1985.

Male explorations

Detailed observations were made for eight males that were observed wandering a distance off of their respective territories (Table 4), exhibiting the stealthy behavior described for exploring male Prairie Warblers (Nolan 1978). One male was observed twice exploring and a second male was observed three different times exploring. In two cases, exploring males began to sing. In both cases, a net, stuffed mount, and song playback were set up with the result being that the males ceased singing and flew off in the direction of their respective territories. Nine of the 11 observed explorations were downstream, toward to the wider portion of the North Fork of Salt Creek.

Table 4. Exploring male distances.

N = 11	Straight distance (m)	Stream distance (m)	Mean distance (m)
Minimum	259	259	259
Maximum	1778	2778	2278
Mean	605	889	752
Standard error	144	378	426
Median	357	481	426

Besides the Prairie Warbler, exploring in other parulids has been observed in males of the Chestnut-sided Warbler (*Setophaga pensylvanica*), Black-throated Blue Warbler (*S. caeruleascens*), Black-throated Green Warbler (*S. virens*), American Redstart (*S. ruticilla*; Kendeigh 1945), Kirtland's Warbler (*S. kirtlandii*; Mayfield 1960), Yellow Warbler (*S. petechia*; DellaSala 1986), Blackpoll Warbler (*S. striata*; Ford 1996), and Pine Warbler (*S. pinus*; Conboy 2011). Nolan (1978) suggests that territorial male exploring behavior may function as part of a dispersal mechanism, giving individuals a way to access the suitability of different sites and contribute indirectly to future territory relocation.

Of the eight male Prothonotary Warblers observed exploring, three (38%) were found to return to a different territory from the previous year. One of these, male #53/1984, returned in 1985 and bred on a site equidistant between the 1984 territory and the exploration site of 1984, suggesting that exploring behavior has an influence on subsequent between-season territory relocation.

Attraction to a specific exploration site was suggested by the case of male #1/1984. This individual was initially captured on 5 May 1984 with an unbanded female, and relocated to a different territory 12 June 1984 and successfully bred on the new territory. This male was observed to leave this territory and explore the same spot on two occasions, 6 June and 7 July.

Reports of exploring parulid males in the literature suggests that the behavior is most common during periods when the opportunity to associate with the mate on the territory is limited, especially during incubation (Kendeigh 1945, Nolan 1978). Nolan

(1978) reports 105 cases of exploring male Prairie Warblers, with 26 being unmated, 20 during egg-laying, and 39 during incubation, representing 81% of the explorer observations. Of the 11 observations of exploring male Prothonotary Warblers on the North Fork of Salt Creek, five of these occurred between 17 May and 21 June, a period during which most Prothonotary Warblers on the study area were nesting (*personal observation*). Of these, two were unmated, two had females who were incubating, and one whose breeding status was not determined. Six explorations were observed between 4 July and 11 July, a period after which most nesting had ended on the study area (*personal observation*).

Exploring males represent a different behavioral category from that of floaters. In contrast to explorers, floaters are wandering non-territorial individuals that are excluded from suitable breeding habitat (Winker 1998). No evidence of floating male Prothonotary Warblers was found on the North Fork of Salt Creek study site. In each year of the study, numerous apparently suitable sites along the stream (Petit and Petit 1996) were unoccupied, suggesting that potential breeding sites were not limiting. In addition, from 1983 to 1986, all territorial males were captured and marked by mid-May and all subsequent observations of exploring males were of known territorial males.

Polygyny

Polygyny has been previously observed in Prothonotary Warblers. Under natural conditions, the reported rate is 1% of all matings (Walkinshaw 1941), while under experimental conditions, with a superabundance of nesting boxes, the rate is 8% (Petit 1991). During this study, three clear instances of polygyny were observed. One case was of a male with two nesting females on his territory. The other two were examples of polyterritorial polygyny (Ford 1996), the first such observation for the Prothonotary Warbler.

Single territory polygyny

In 1984, male #58/1984 and female #1/1984 (M1 and F1) and male #56/1984 and female #23/1984 (M2 and F2) occupied adjacent territories. On 11 June 1984, five young were fledged on the territory of M1 and F1. Both adults were observed feeding the fledglings until 14 June, after which F1 was no longer observed on the territory. On 15 June, F1 was observed on the territory of M2. M1 attempted to follow her and was chased off by M2. M1 was last seen feeding fledglings on 16 June. M1 was not observed on the territory again until 11 July, where he remained until 25 July, unmated and in molt.

On 23 June, M2 and F2 were observed feeding a group of three fledglings. On that day, F2 alternated between feeding fledglings and placing nesting material in a cavity in a dead stump, 5 m inland from the stream. On 11 July, F2 was observed feeding nestlings at this nest site. During 3 h of observation that day, M2 never brought food to this nest, but rather was observed bringing food and removing fecal sacs along with F1 from a nest containing four nestlings, 15 m from the nest of F2. The nest of F1 fledged on 16 July, and on 19 July M2 was observed to alternate between feeding the fledglings and bringing food to the nest of F2. F2's nest fledged on 24 July, and on that date, M2 and both females were observed in the company of fledglings. On 27 July, M2 was observed in the company of two fledglings, but neither female was noted.

Polyterritorial polygyny

Polyterritoriality, the simultaneous holding of two or more disjunct territories with associated polygynous matings, has been reported for six species of parulids (Secunda and Sherry 1991, Ford 1996, Conboy 2011; Bocetti, *personal observation*). Two cases of polyterritorial polygyny were observed on the North Fork of Salt Creek, representing the first such observations for the Prothonotary Warbler.

Male #33/1983 was first banded on 7 July 1983, feeding fledglings on territory A. On 8 May 1984, this male was recaptured on territory A and was accompanied by an unbanded female. On 9 May 1984, this individual was recaptured with song playback in the company of an unbanded female at territory B. Territory B was located 519 m upstream (straight line distance) from territory A. This male was observed on territory B on 6 June 1984 with an unbanded female that was observed entering a cavity and remaining, suggesting that the female was incubating. The apparent nest site at territory B was inaccessible. On 7 June 1984, male #33/1983 was observed back on territory A. A nest was located, with five eggs, and the incubating female was subsequently captured and marked. This nest was checked on 25 June 1984 and was found to have been predated. The marked female was not further observed. On the same day, the male was back on territory B, and was captured at song playback. The fate of the territory B nest was not determined.

Male #62/1983 was captured by song playback on 2 June 1983 on territory C. On this date, his mate was captured and marked while incubating. On 5 June 1983, this male was captured by use of song playback on territory D, 429 m downstream from territory C and with an unbanded female who was apparently incubating in an inaccessible nest cavity. The fate of these two nests were not determined.

In both cases, males observed travelling in between the two territories were never observed to sing until they were on one or the other of the two territories, nor did they respond to song playback while in between territories. The stretch of stream between territories, in both instances, was unoccupied by other male Prothonotary Warblers. Table 5 compares the distances between concurrently held territories of the males in this study with those reported in the literature for other polyterritorial parulids.

Homing

On 9 June 1985, four unmated territorial males were captured by song playback. Three of these were first banded on that date while one, male #45/1984, was banded the previous year on the same territory, where he successfully fledged young in 1984. The birds were transported in opaque paper bags and released at a site on the West Fork of the White River in Morgan Co., Indiana, USA, 47 km due north of the North Fork of Salt Creek study area. The release site was in a separate drainage from that which feeds the North Fork of Salt Creek. Four days later, on 13 June, male #45/1984 was recaptured back on his territory with song playback. The other three relocated males were never again observed.

Long distance homing back to the breeding territory by male passerines has been reported in the Song Sparrow (*Melospiza melodia*; Manwell 1936), Red-winged Blackbird (*Agelaius*

Table 5. Distances between concurrently held territories of polyterritorial parulids.

Species	Straight line distance(s) (m)	References
American Redstart (<i>Setophaga ruticilla</i>)	94/150/200	Secunda and Sherry 1991
Black-throated Blue Warbler (<i>S. caerulescens</i>)	300	Petit et al. 1988
Kirtland's Warbler (<i>S. kirtlandii</i>)	300 to 400	Bocetti, <i>personal observation</i>
Pine Warbler (<i>S. pinus</i>)	398	Conboy 2011
Prairie Warbler (<i>S. discolor</i>)	100/1300	Nolan 1978
Prothonotary Warbler (<i>Protonotaria citrea</i>)	429/519	This study
Yellow Warbler (<i>S. petechia</i>)	200	Ford 1996

phoeniceus; Manwell 1941), Brown-headed cowbird (*Molothrus ater*; Manwell 1962), and Dark-eye Junco (*Junco hyemalis*; Nolan et al. 1986). The only other report of homing for a parulid is that of a male Prairie Warbler released 4.8 km north of the territory and returning to the territory 24 h later (Nolan 1978).

DISCUSSION

The presence of “floaters,” non-territorial individuals prevented from breeding by the unavailability of suitable territories (Winker 1998), has been suggested by studies starting with the large-scale removal experiments of Hensley and Cope (1951) and Stewart and Aldrich (1951). However, in these and other removal experiments, the previous status of the replacement males was often not known and could have been exploring territorial males from nearby areas (Thompson 1977, Nolan 1978, Morse 1989). The best evidence for the existence of male floaters in parulids, limited by available territories, is that for Ovenbirds (*Seiurus aurocapilla*; Bayne and Hobson 2001). In this study, the authors attribute the existence of floaters to the unusually high density of Ovenbirds on their Saskatchewan study site.

A second explanation for the reoccupation of vacant territories by males is that these males are nearby territorial individuals attracted to the new territory by the presence of “widowed” females. This notion is strongly supported by the removal experiments performed on Black-throated Blue Warblers by Marra and Holmes (1997).

During this study, no evidence was found suggesting the presence of a population of floater male Prothonotary Warblers on the North Fork of Salt Creek. By mid-May of the seasons 1983 to 1986, all territorial males present on the study area had been captured using song playback with a stuffed mount. Subsequent observations of males, including exploring males, were of known marked individuals. In addition, during each year of the study, numerous spots of apparently suitable Prothonotary Warbler habitat (Petit and Petit 1996) were unoccupied, suggesting that the population of male Prothonotary Warblers on the North Fork of Salt Creek was not limited by the availability of suitable habitat. As is the case for other North American breeding parulids (Morse 1989), male Prothonotary Warblers arrive at the breeding grounds two to seven days before females (Bent 1953; *personal observation*)

and select sites based upon the presence of suitable nesting cavities (Petit 2020). Newly arrived males will choose a cavity to add nesting material, usually moss, to construct a “dummy” nest (Bent 1953), which, on some occasions, is chosen by the female as the site of the first nesting (Walkinshaw 1953). Again, the presence of unmated territorial males along the North Fork of Salt Creek suggests that the unavailability of females was a more important factor than was the lack of suitable territories.

The observation of extraterritorial explorations by male Prothonotary Warblers on the North Fork of Salt Creek study area represents a behavior of particular interest. Nolan (1978) suggests that explorer behavior by male Prairie Warblers plays a role in the process of territory relocations and is part of a general dispersal mechanism in that species. Observations of exploring Prothonotary Warbler males in this study suggests that exploration influences within- and between- season territory relocations, with male Prothonotary Warblers tending to explore toward the downstream section of the study area, along with some individuals showing attachment to particular exploration sites.

Hoover (2003) found that between-year site fidelity in both male and female Prothonotary Warblers is strongly influenced by nesting success in the previous season, with over 80% of individuals who successfully nested twice returning to the same site the following year. In addition, he found that 51% of reproductively unsuccessful males returned to the same territory if their neighbors successfully raised young as opposed to a 16% return rate for males whose neighbors were unsuccessful. This influence of neighbor reproductive success on site fidelity has been previously reported in other species (Bollinger and Gavin 1989, Doligez et al. 2002, 2003). In this context, extraterritorial exploration behavior by male Prothonotary Warblers would be a mechanism that would allow an individual to access the reproductive status of neighbors.

Given that the availability of suitable Prothonotary Warbler habitat in a natural situation can change abruptly, even within a season, extraterritorial exploration is clearly an adaptive behavior. Flooding (Flaspohler 1996), loss of decayed nesting trees (Petit 2020), or predator damage to nesting cavities (*personal observation*) has the potential to quickly render a particular territory unsuitable.

Exploring behavior by territorial male parulids is probably more common than generally realized (Nolan 1978, Morse 1989, Webster et al. 2001, Pederson et al. 2006, Churchill and Hannon 2010). During this study, no observations were made of female Prothonotary Warblers showing behavior consistent with exploring. However, covert female parulid exploration may also be common. Using radio-tracking, Neudorf et al. (1997) found that 80% of the female Hooded Warblers (*Setophaga citrina*) on their study area performed extraterritorial forays and these being done during their respective fertile periods, with resulting extrapair copulations.

Radio telemetry studies have shown that the distances covered by explorers are greater than is normally suspected. Male Kirtland's Warblers have been observed to explore 5 km to 77 km from their territories with 65% of the movements being nocturnal (Cooper and Marra 2020) and male Grasshopper Sparrows (*Ammodramus savannarum*) explore up to 9 km from the breeding territory

(Williams and Boyle 2018). That male Prothonotary Warblers are capable of similar movements is suggested by the homing experiment performed during this study, where a male, displaced 47 km, returned to his territory, and this from a different river system. To reach the North Fork of Salt Creek territory, this male would have had to traverse a large area of unsuitable Prothonotary Warbler habitat. The mechanism controlling this example of homing would appear to be different from that which operates during spring migration in this species, where Prothonotary Warblers follow riverine habitat on their way north (Butler 1898, Parnell 1969, Petit 2020).

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Data Availability:

No data/code were analyzed in this study.

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