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Monitoring the long-term nesting success, site fidelity, and population dynamics of a neotropical migratory bird: Implications for floodplain restoration

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Location of Research: Cypress Creek National Wildlife Refuge (USFWS), and the Cache River watershed

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Annual Report

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INTRODUCTION

Large-scale (entire watershed) restoration projects are uncommon. Long-term studies of vertebrate populations are rare (Cody 1996). Long-term studies of populations occurring within a large area that is currently being restored are nearly nonexistent. The importance of long-term studies, however, can not be overstated (Cody 1996). For neotropical migratory birds, long-term studies of marked individuals allow scientists to track populations over several years and to follow some individuals for the duration of their life. Long-term studies allow one to document annual variation in parameters important to migratory birds (e.g.; weather, food resource availability, nest predation, brood parasitism), and result in a greater understanding of how annual variation (or lack thereof) influences the reproductive success and survival of individuals, and the maintenance and stability of populations. Habitats can also change over time, and habitat fragmentation has been associated with increases in nest predation and brood parasitism that prevents residual habitat fragments from being productive enough to maintain populations of birds (Robinson and Hoover 1995, Hoover et al. 1995, Robinson et al. 1995).

Less is known, and little has been documented, concerning how large-scale habitat restoration occurring over a long period of time affects populations of songbirds. Management recommendations for restoration projects are often based more on speculation and less on actual data gathered from the area undergoing restoration. Often, research and management actions are not integrated with each other or with continued monitoring (DeSante and Rosenberg 1998). Long-term studies that track habitat restoration and the resulting responses of the avian community are invaluable because they provide insight into the natural processes that affect the function and value of habitat for songbirds and other organisms, and how these processes change over time. The long-term nature of such studies also allows for specific management-oriented questions to be addressed.

The Cache River Wetlands (CRW) project, including the Cypress Creek NWR, continues to provide a unique opportunity to incorporate the results of songbird research within the restoration project area into management recommendations in the short-term. These recommendations will be validated in the long-term with future research during the progression of the restoration. In the CRW area, previous research has established the importance of connecting and enlarging existing tracts of forest (Robinson and Hoover 1995), of restoring and managing a wide variety of floodplain habitats (Hoover and Robinson 1996), of restoring and/or managing water levels at particular levels during critical periods during the breeding season (Hoover and Robinson 1997, and forthcoming Accomplishments Report for 1998), and that site fidelity and population dynamics of neotropical migrants are influenced by nest predation resulting from nest predator responses to fluctuations in water levels during the breeding season.

The primary source of information used to determine the community-wide responses of birds to habitat restoration is census data. This data can be used to document species richness, abundance, community composition, and any changes in these factors over time. A focal species is required, however, in order to obtain information on nesting success, nest predation, and brood parasitism over a wide area within a given year, and over several years (especially where habitat is changing due to restoration) (Temple and Wiens 1989). Specific questions relating to natural processes (brood parasitism, nest predation, and hydrology) can also be addressed by studying a focal species. Long-term studies of marked populations of a focal species are necessary to obtain information regarding site fidelity, local dispersal, natal philopatry, source/sink dynamics, population dynamics, turnover rates, lifetime productivity, and survival rates (DeSante 1995).

The Prothonotary Warbler (Protonotaria citrea) is an ideal focal species to use for a long-term study, especially within an area where a vast amount of floodplain forest

restoration is occurring. We have been studying 150-200 pairs of color-marked warblers within the CRW and Cypress Creek NWR from 1994 to the present. The Prothonotary Warbler is a floodplain and swamp (wet) forest specialist that nests in secondary cavities and has experienced significant population declines during the past 30 years (Sauer et al. 1997). Prothonotary Warblers preferentially nest over water (Petit and Petit 1996, J. Hoover, unpubl. data), their nests are usually located 1-2.5 m above ground (or water) level, they are abundant in a variety of wet forested habitats in the CRW area, they are easy to capture and color-band, and they readily use nest boxes. Their nests (natural cavity and nest box) are preyed on by numerous species of nest predators including Raccoons (Procyon lotor), mice, snakes, Southern Flying Squirrels (Glaucomys volans), and avian nest predators. The identity of nest predators responsible for each predation event can be determined > 95% of the time (J. Hoover, unpubl. data), and this information can provide a relative index of nest predator activity among the many study sites and habitat types within the CRW. Prothonotary Warblers are also parasitized quite heavily by Brown-headed cowbirds (Molothrus ater), and this information can provide a relative index of brood parasitism throughout the CRW. More importantly, rates of nest predation and brood parasitism can be tracked over the long term to determine if and how they change as restoration occurs.

There are many advantages to studying a species nesting in nest boxes. Individuals (especially females) are easier to capture when the location of the nest is known. Also, detailed information on the productivity of individual birds can be obtained (clutch size and composition, hatching success, brood size and composition, fledging success, number of nesting attempts, and number of broods fledged). One concern when studying birds that nest in nest boxes is that nesting success in nest boxes may not be similar to that in natural cavities. In this study, the fates of Prothonotary Warbler nests in nest boxes is similar to that in natural cavities (n = 1,750 and 103 nests in nest boxes and natural cavities,

respectively) and they experience similar rates of brood parasitism and nest predation in each (J. Hoover, unpubl. data). There are possibly subtle differences between nests in nest boxes and natural cavities, but these differences are relatively unimportant to our primary results in this report. Another advantage to studying a species that nests in nest boxes is that the amount of habitat sampled and the sample size of active nests in a single breeding season can be very large.

We now know that the rate and amount of water level fluctuations during the breeding season influence the rate of nest predation, in turn affecting season-long productivity and ultimately influencing the patterns of site and territory fidelity of birds breeding in bottomland and swamp forests. This suggests that the birds are able to avoid returning to sites that have low reproductive success due to high rates of nest predation (sink habitat), but only after experiencing an entire breeding season on such a site. Site fidelity and territory fidelity are high to areas that have high reproductive success (low rates of nest predation). Brood parasitism and the raising of cowbird young, however, has no influence on site fidelity for Prothonotary Warblers. This suggests that sites that qualify as sink habitat because of brood parasitism by cowbirds are potentially acting as ecological traps. What remains to be determined is whether or not individual warblers make decisions each breeding season regarding returning the following year. Most of the study sites in the CRW area experience much between-year variation in water level fluctuations and the resulting rates of nest predation and it would be adaptive if the birds were capable of responding to this between-year variation over the course of their lifetime.

With the continued long-term monitoring of these color-marked populations of Prothonotary warblers, we addressed the following questions: (1) Do individual warblers respond to between-year variation in water levels (and nest predation) by deciding each year throughout their reproductive lifetime whether or not to return to a site based on the

previous year's breeding success? (2) How do local populations respond to one year or to 2 or more consecutive years of high nest predation and low nesting success? (3) Based on current data relating reproductive output to water levels, can sites be easily and accurately classified as source or sink habitat by only measuring water depths during the breeding season? (4) Have rates of brood parasitism changed any from those in 1993-1994, as several thousand acres of land in the CRW are now 2-6 years post-agriculture? (5) What are the survival rates, life expectancies, and lifetime reproduction values for Prothonotary Warblers nesting in the CRW? (6) What are the patterns of natal philopatry for warblers produced in the CRW?

OBJECTIVES

(1) Continue long-term monitoring of Prothonotary Warblers in the Cypress Creek NWR and the CRW, including site fidelity, brood parasitism and nest predation.

(2) Continue monitoring population dynamics of Prothonotary Warblers among the study sites and relate fluctuations in populations to reproductive success and hydrologic variability in previous years.

(3) Categorize sites within the Cypress Creek NWR and CRW as source or sink habitat for Prothonotary Warblers based on reproductive output as influenced by fluctuations of water levels during the breeding season.

(4) Use the long-term return data that is being obtained in the Cypress Creek NWR and CRW to determine the survival rates and life expectancies for Prothonotary Warblers.

(5) Continue gathering data on natal philopatry.

(6) Use these data to provide recommendations for restoration and management of bottomland and swamp forests in the Cypress Creek NWR and the CRW.

METHODOLOGY AND STUDY DESIGN

(1) We captured all adult Prothonotary Warblers on 23 study sites and banded each unmarked individual with a unique color-band/USFWS aluminum band combination. Males were captured using a mist net, decoy, and taped play-back of a male song. Females were captured while in the nest box. When adults were captured, we determined their age based on morphological characteristics and feather wear. We followed individuals throughout the breeding season and recorded, for each individual, nest-site location(s) and reproductive output. Prothonotary Warbler nestlings were banded with a USFWS aluminum band when they were 8-9 days old (approx. 2-3 days before fledging). We compared site fidelity of individuals in 1999 to their reproductive histories from the previous breeding season.

(2) We measured water levels (depth) every 4 days from 1 April to 15 August beneath a total of 1,200 nest boxes placed among 23 sites in the following habitats: natural levees along the Cache River; swamps with consistently deep water; swamps maintained by beavers; ephemeral natural swamps with shallow water; and sites experiencing rapid and/or large water-level fluctuations. Nest boxes were made from 1.9 liter milk and juice cartons (Petit 1989), and placed 1.7 m above ground on trees. We monitored nest boxes every 4 days coinciding with water level measurements. For all predation events at nest boxes, we identified the nest predator and documented the depth of the water beneath nest boxes at the time of predation. For each nest we have a record of nesting activity and fate of the nest.

(3) We determined how consistently sites within the Cypress Creek NWR and the CRW act as source, stable, or sink habitats (Pulliam 1988) to determine the extent of between-year variation in habitat quality. We used the known productivity of individuals and estimates of adult and juvenile survival (based on returns of marked individuals) to determine whether or not a site was a source in a given year. We compared between-year

site fidelity of adults to habitat quality and determined whether or not adults are adaptively returning to good habitat and avoiding poor habitat.

(4) We used both correlative and experimental mark and recapture data from 1997-1999 to estimate survival rates and site fidelity, and data from banded warbler nestlings (1995-1999) to obtain information on natal philopatry. We compared the site fidelity for experimental populations (where nesting success was manipulated so that individuals were randomly assigned 0, 1, or 2 broods as their productivity for that breeding season) for two years (1997-1998 and 1998-1999). We also compared site fidelity of individual adult warblers between experimental and non-experimental (correlative) groups during the same time period (1997-1999). We compared natal philopatry (warblers produced in the watershed that return to the watershed as breeding adults) between males and females, between nestlings with and without a cowbird nestmate, and between nestlings produced early vs. late in the breeding season.

(5) We continued the long-term monitoring of the avian community throughout the CRW by conducting point counts (Hutto et al. 1986) on several sites that have been censused each year since 1993. We also obtained detailed information on nest predation and brood parasitism of Prothonotary Warblers for sites that have been monitored since 1994. This information will be used to determine what short-term effects have resulted from the restoration process (land acquisition and planting) during the past 6 years.

RESULTS AND DISCUSSION

During the 1999 summer field season we studied approximately 200 pairs of Prothonotary Warblers distributed among 23 study sites. Out of these 200 pairs, 182 females and 153 males were color-marked, with the remainder not being captured. Nesting success for the Prothonotary Warblers was higher in 1999 than during the previous two

years and 303 warbler nestlings were banded prior to their fledging from nests. This increase in nesting success is a result of the rainfall and subsequent water-level fluctuations that occurred during the 1999 breeding season.

Prior to this year, nesting success had been relatively high in 1995 and 1996 in years where the Cache River watershed received a lot of rain in the spring and throughout the summer and water levels remained deep (> 30 cm) for a substantial portion of the breeding season. In 1997 and 1998, spring flooding was followed by several repetitions of water drawing down on and reinundating study sites. These fluctuations throughout the summers of 1997 and 1998 exposed the warbler nests to predation by Raccoons during the numerous instances when the depth of water beneath the nests dropped below 30 cm. The pattern of water-level fluctuation during the 1999 breeding season was unlike any of the previous four years.

In 1999, spring flooding filled all of the study sites with normal amounts of water. This initial pulse of water was present when the warblers settled onto territories in the spring, and all sites were occupied as in the previous four years. The water then slowly drew down on most of the study sites, exposing the warblers to high rates of nest predation by Raccoons when the water depth beneath nests became less than 30 cm. Many of the study sites then dried up and were not reinundated with water for the remainder of the summer (early June through July). Nest predation by Raccoons decreased as the sites became dry, and rates of nest predation remained at low levels as long as a site was not reinundated with water. Also, nests along the Cache River on the natural levee experienced relatively high rates of nesting success because the Cache River stayed far down inside its banks for the latter two thirds of the breeding season. Higher rates of nest predation occur along the natural levee when the river is flowing at the top of its banks and Raccoons are moving along the river edge. The continued study of these populations of warblers in the

Cache River watershed is allowing us to document the variability of water-level fluctuations over several years and how this variation influences the nesting success of Prothonotary Warblers by influencing the movement and foraging behavior of Raccoons.

A two-year experiment studying the site fidelity of Prothonotary Warblers was completed during the 1999 breeding season. We now know that the number of broods an individual warbler produces is the primary factor influencing between-year site fidelity for that individual. During the summers of 1997 and 1998, we experimentally manipulated nesting success and randomly assigned individuals to produce zero, one, or two broods. This experiment was successfully accomplished by conducting the experiment on study sites known to have high rates of nest predation and by predator proofing (against Raccoons) the nest boxes of those individuals that were to produce one or two broods. The result of this experiment was that between-year site fidelity increased with an increase in the number of broods an individual warbler produced (zero, one, or two) for both males (Fig. 1) and females (Fig. 2) with nearly 80% of those individuals that produced two broods in one year returning to the same site the following year. These results were similar to the patterns of between-year site fidelity during the same two years for warblers nesting on study sites where no experimental manipulations occurred (correlative data) for both males (Fig. 3) and females (Fig. 4). These results indicate that high rates of nesting success promote high returns of adult warblers between years, and high returns may promote stable populations. The results of the experiment also indicate that annual survival rates for adult Prothonotary Warblers may be between 70-80% (based on return rates of the experimentally manipulated individuals producing 2 broods).

At the end of the 1999 breeding season, the total number of Prothonotary Warblers that were banded as nestlings (1995-1998) and subsequently returned to one of the study sites as breeding adults (1996-1999) was 39. This total included 25 females and 14 males.

The distributions of natal dispersal distances are given in Figure 5 for males and females separately. All of the natal dispersal distances are between 0 and 9,500 m, and no nestlings have returned to the specific territory where they were produced. Sample sizes are presently too small for statistical analysis, but the general trend appears to be that males disperse shorter distances (> 50% within 1,000 m of where they were produced) than females (> 50% within 1,000-2,500 m of where they were produced) (Fig. 5). Natal philopatry (the return of birds to the area where they were produced) was not influenced by having cowbird nestmates (Fig. 6) or by being produced during the early or latter part of the breeding season (Fig. 7).

Cowbird parasitism usually results in lower hatching success and brood reduction in Prothonotary Warbler nests and these costs of brood parasitism increase with increasing levels of parasitism. However, it appears that if a warbler nestling survives and fledges from a nest, it has a similar chance of returning in a subsequent year regardless of whether it came from an unparasitized nest or a nest with one or two cowbird nestmates (Fig. 6). Nestlings produced early in the breeding season disappear from the study sites within two weeks after they fledge. We had hypothesized that these individuals would be less likely to return to the watershed as they may disperse greater distances prior to migration than do those nestlings that fledge later in the breeding season and stay within the watershed until closer to the time of migration. The results of our early vs. late analysis do not support this hypothesis (Fig. 7). With two more years of data on natal philopatry and dispersal we will have adequate sample sizes to address several questions regarding the factors influencing natal dispersal distances. Prior to this long-term research project, this information has rarely been obtained for migratory birds.

Brood parasitism by cowbirds continues to be prevalent throughout the Cache River watershed, but some interesting trends are becoming apparent with the addition of each year

of data collected (Table 1). Rates of brood parasitism continue to be high in Buttonland Swamp where there are few alternate host species and cowbirds are very abundant. Rates of brood parasitism were relatively low in 1999, however, in Hickory Bottoms, Add's Branch Corridor, and Main Tract. These sites are all embedded within extensive areas of land that have been acquired during the previous 7 years and are now some years into the process of succession from field to forest. Some of the study sites within the most extensive area of bottomland forest in the watershed (Heron Pond/Little Black Slough) continued to have predictable low rates of brood parasitism with the exception of the Heron Pond study site where all of the nests are located within 3 km of an extensive cattle pasture (Table 1). In 1999 we also added new study sites in forest adjacent to the newly acquired Grassy Slough Preserve (a 2,200 acre block of land that was farmed for the last time in 1999) and are now poised to document any changes in parasitism as the land is restored. This will give us direct measures of short-term changes in brood parasitism as restoration progresses.

We now have productivity data (number of young produced per color-marked female warbler per year) for several sites over five years (Table 2). To classify these sites as either sources (production in excess of losses to mortality) or sinks (production less than losses to mortality) we need to know productivity, annual survival rates of adults, and a juvenile survival rate (Pulliam 1988). The source/sink theshold occurs where [(adult survival) + (juvenile survival)(female young produced per female)] is equal to one. Using the data collected from the site fidelity experiment and from the overall returns of individuals over the years of this study, a conservative estimate of adult survival for Prothonotary Warblers (both male and female) is 70%. Juvenile survival is often estimated as half of adult survival (here 35%). Given these two values, the source/sink threshold occurs where the number of female young produced produced per female is 0.85. Our values for productivity are total number of young produced (males + females) and thus the

source sink threshold occurs where these values of productivity are (2)(0.85) or 1.70. Values of productivity above and below 1.70 are sources and sinks, respectively.

During the years 1995-1999, only one study site (BS) has consistently been a source (Table 2). Much of this site has deep (>30 cm) water for the duration of each breeding season and subsequently has low rates of nest predation (Raccoons do not forage in deep water). Two sites (CM and ABC) have been sinks each year. These two sites have predictably shallow (< 30 cm) water for the duration of each breeding season and high rates of nest predation by Raccoons. Other sites are sources some years and sinks in others, depending on water-level fluctuations on each study site in a given year. Overall (all sites combined), the watershed was a source for Prothonotary Warblers in 1995 and 1999 (Table 2). The watershed was at the source/sink threshold in 1996 and was a sink in 1997 and 1998. At the scales of study site and watershed, sources are more prevalent in years when water levels remain high throughout much of the breeding season, or in years when water levels drop after the initial spring flooding and sites remain dry for the remainder of the breeding season (see above discussion of water-levels and nest predation). The percentage of sites that are sources in a given year is highly variable among the five years (Table 2), and is also related to rates of nest predation by Raccoons that are influenced by water-level fluctuations during the breeding season.

The age structure of the breeding population in the Cache River watershed included males and females from 11 and nine age categories, respectively (Table 3). The age structure for males and females was similar for third-year (TY) and older birds. The percentage of birds in the second-year (SY) and after-second-year (ASY) age categories differed between males and females. These two categories (SY and ASY) represent the individuals that were new to the study area (unbanded). SY birds are breeding for the first time (they were produced in the previous breeding season) and ASY birds are at least one

year older than SY. The majority of "new" males in the population are breeding for the first time whereas the majority of "new" females are older than SY and attempted to breed somewhere else in the previous year (and were likely unsuccessful the previous year). This difference between males and females may be influenced by the patterns of site fidelity that we documented with our site fidelity experiment. Unsuccessful females return to sites between years at a low rate relative to that of unsuccessful males (Figs. 1 and 2). The unsuccessful females not returning between years (and that are still alive) are dispersing to different sites the following breeding season. The large amount of ASY females entering the Cache River watershed populations in 1999 may indicate that nesting success was poor in 1998 in areas within the watershed where we are not studying the warblers and/or in areas surrounding the watershed.

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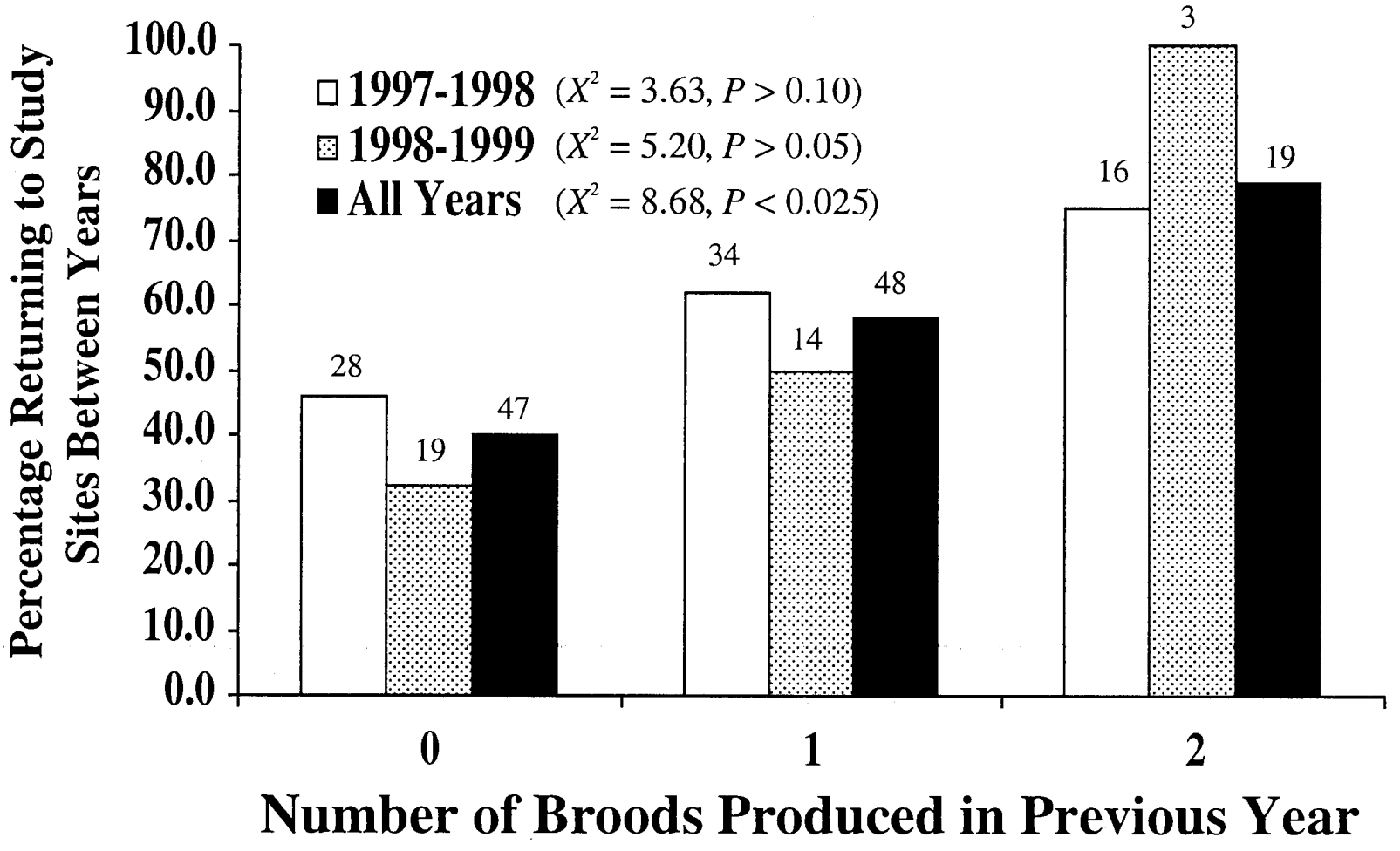

Figure 1. **Experimental** patterns of between-year **site** fidelity for **male** Prothonotary Warblers in the Cache River watershed (numbers above bars indicate sample sizes).

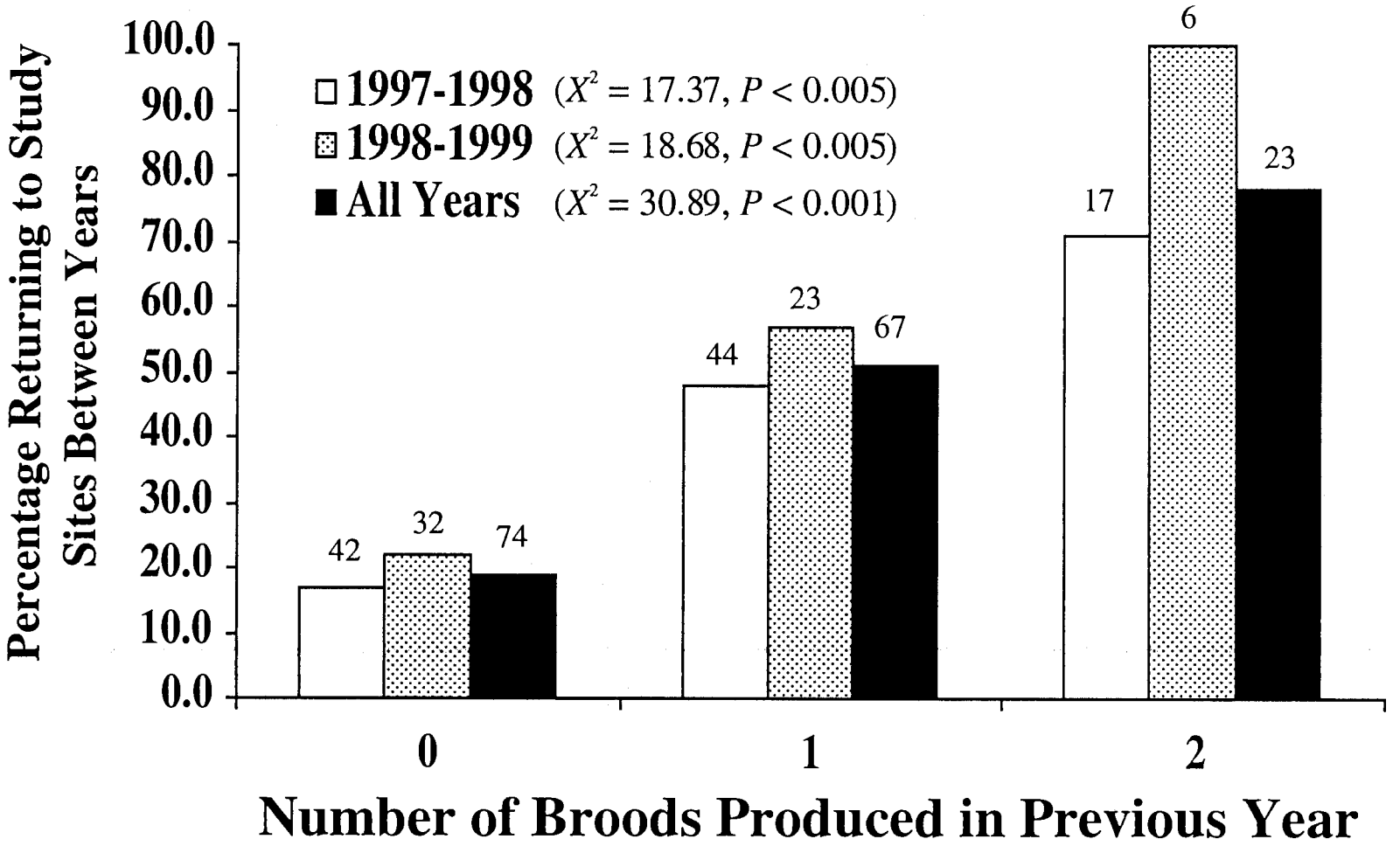

Figure 2. **Experimental** patterns of between-year **site** fidelity for **female** Prothonotary Warblers in the Cache River watershed (numbers above bars indicate sample sizes).

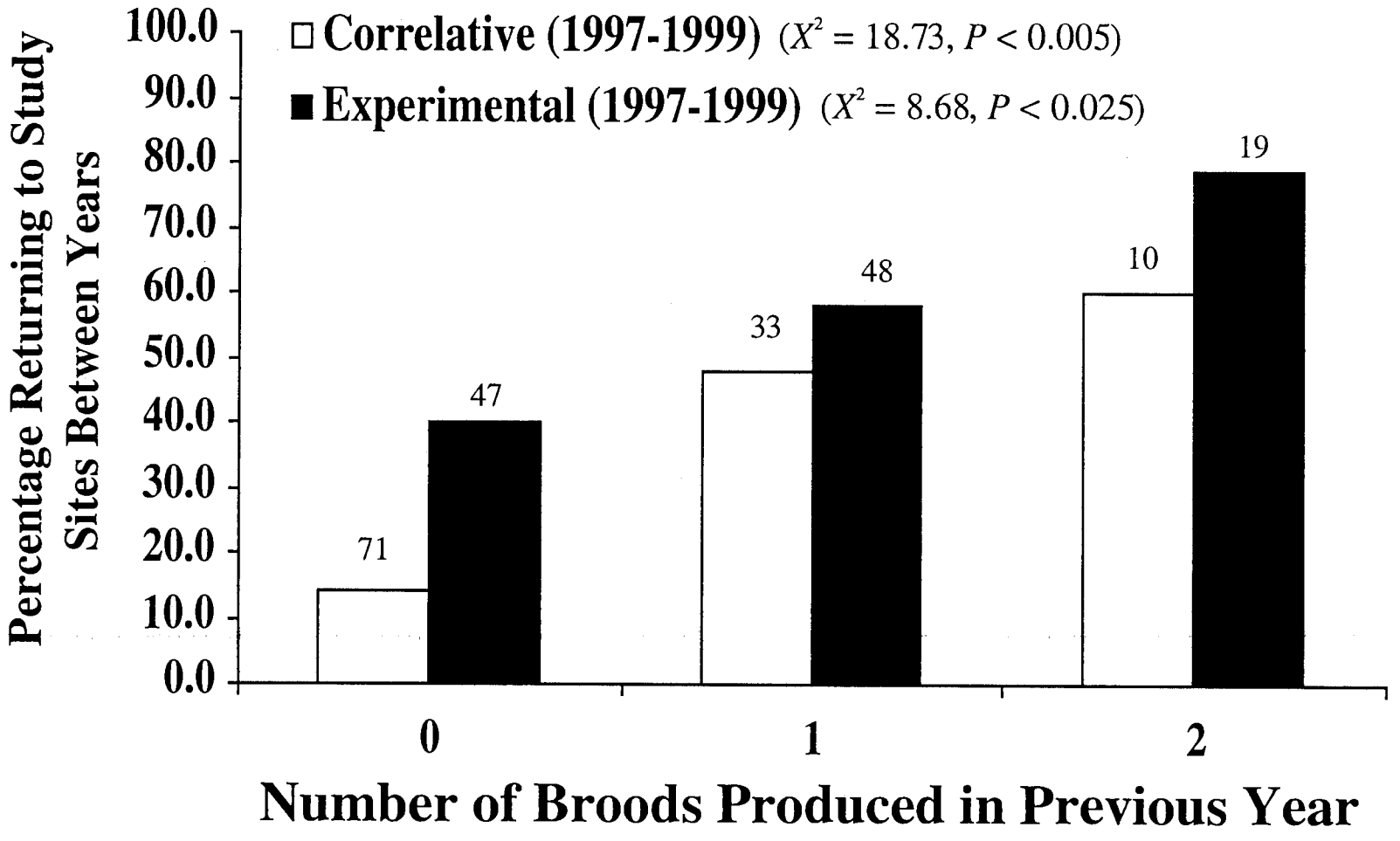

Figure 3. A comparison of correlative and experimental patterns of between-year **site** fidelity for **male** Prothonotary Warblers in the Cache River watershed (numbers above bars indicate sample sizes).

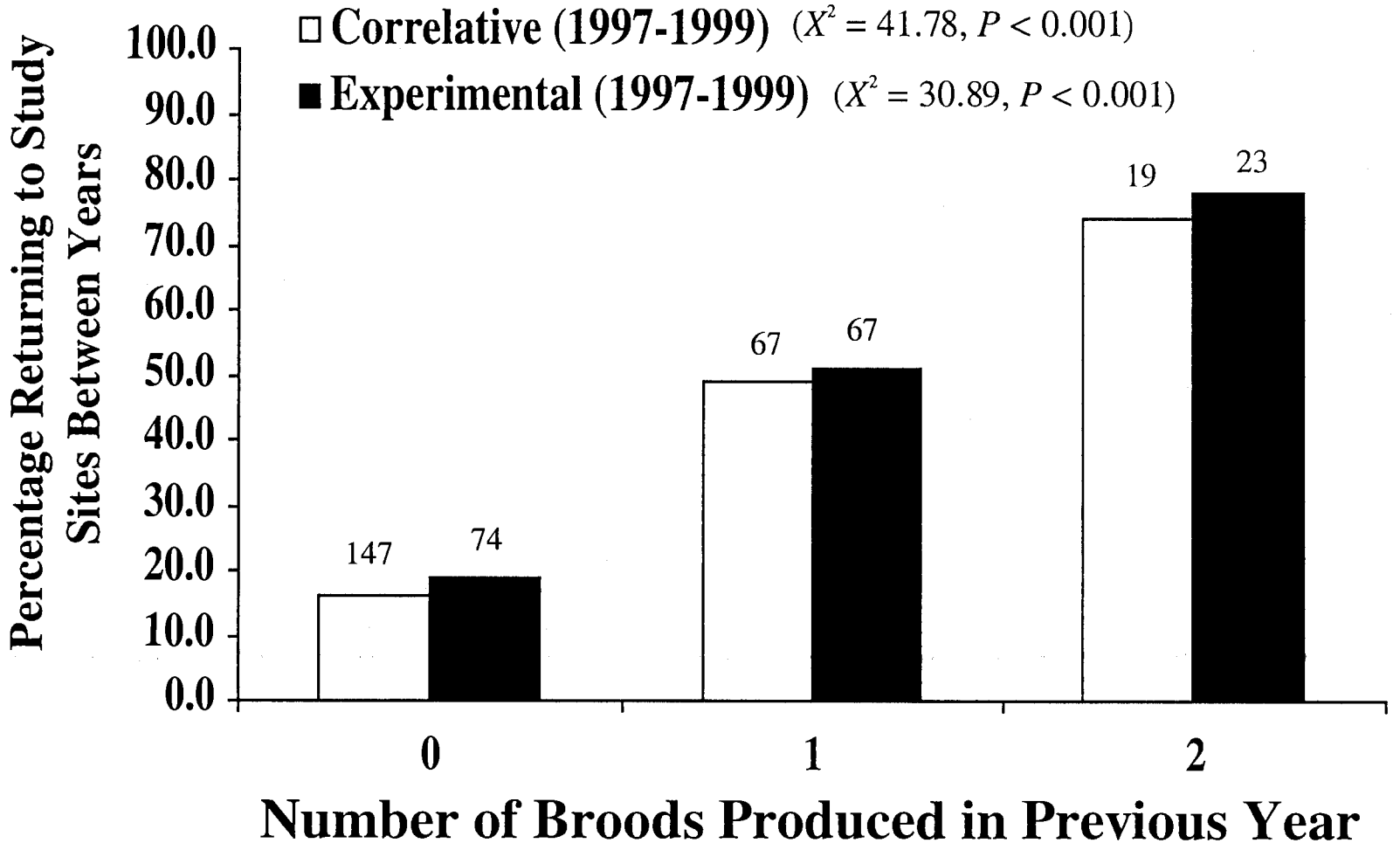

Figure 4. A comparison of correlative and experimental patterns of between-year **site** fidelity for **female** Prothonotary Warblers in the Cache River watershed (numbers above bars indicate sample sizes).

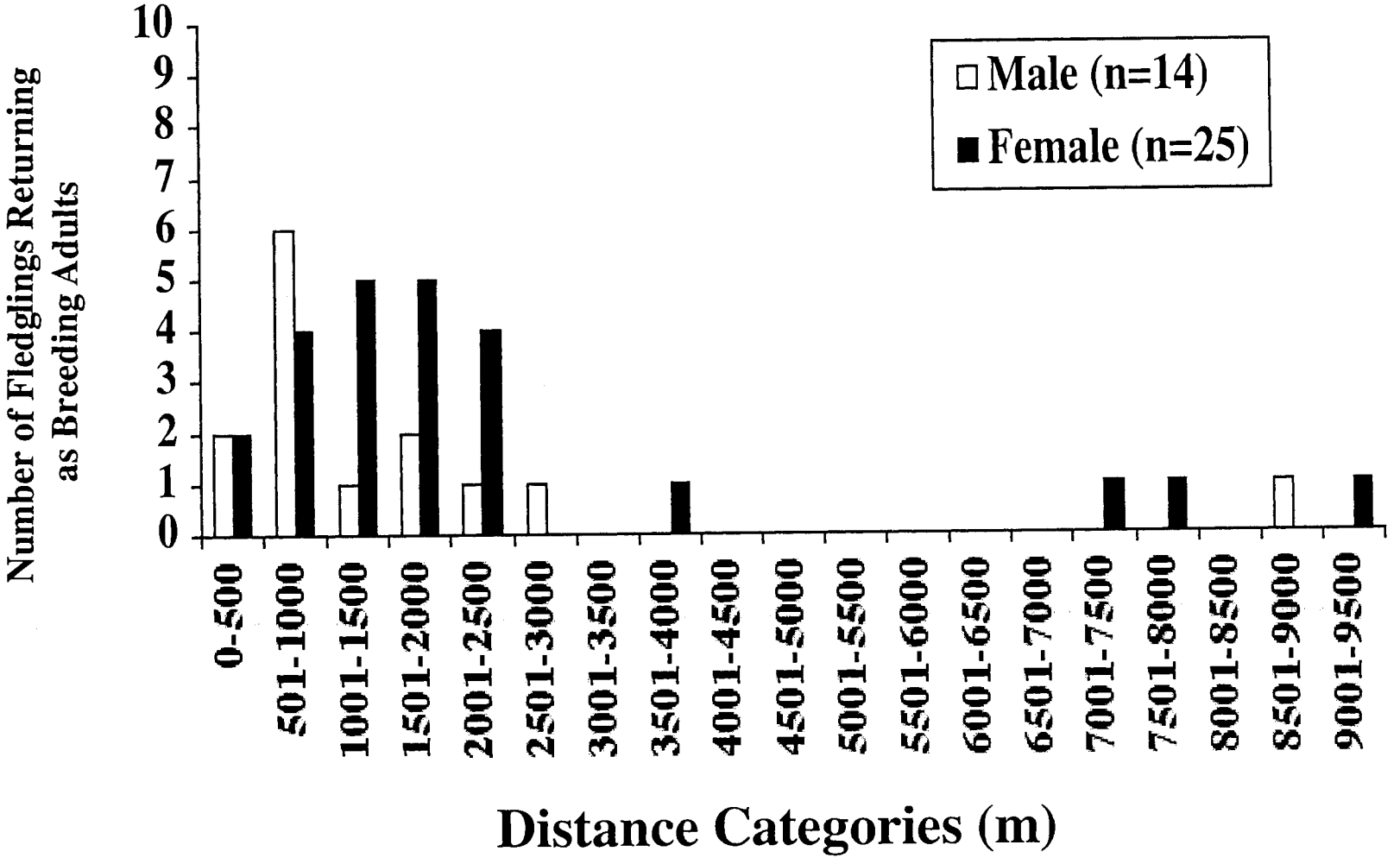

Figure 5. Distances between place of fledging and subsequent place of breeding for Prothonotary Warblers banded as nestlings in the Cache River watershed (1995-1998) and returning as breeding adults to the Cache watershed (1996-1999).

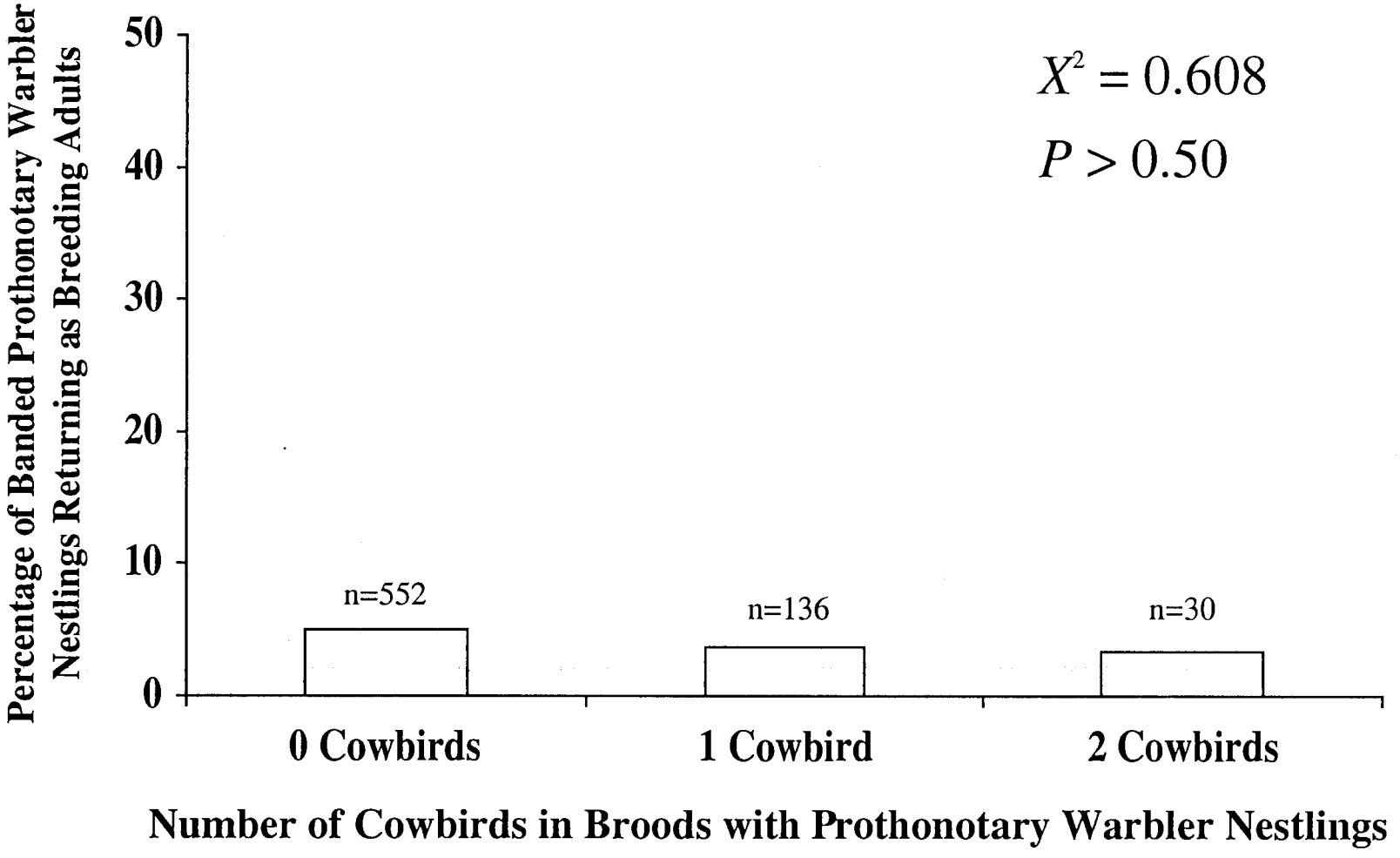

Figure 6. A comparison of natal philopatry for Prothonotary Warbler nestlings that fledged from broods containing 0, 1, or 2 cowbird nestlings in the Cache River watershed (1995-1999) (sample sizes given above bars).

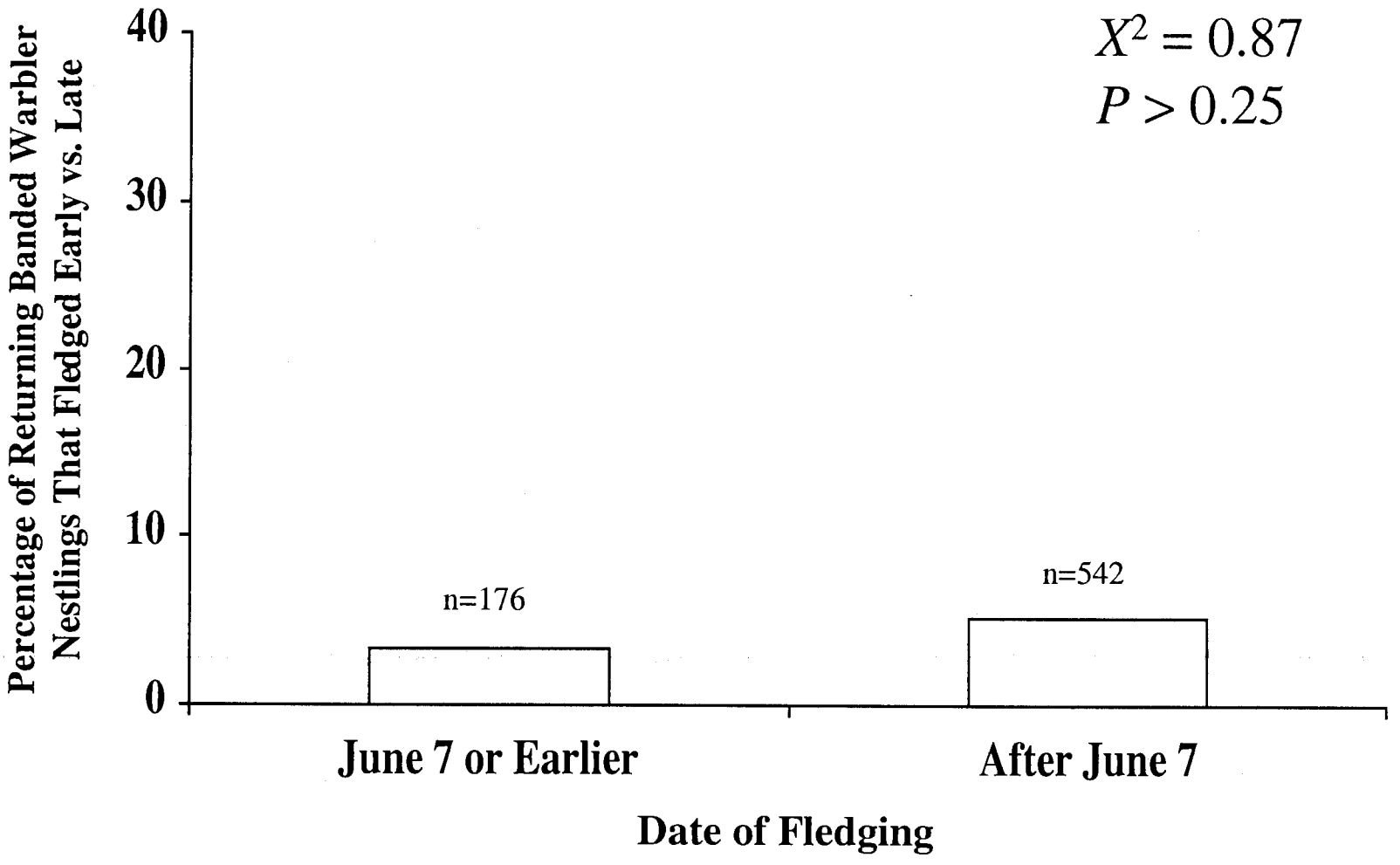

Figure 7. The percentage of banded Prothonotary Warbler nestlings that fledged during the early or late portion of the breeding season and returned as breeding adults in a subsequent year in the Cache River watershed (1995-1999) (sample sizes given above bars).

Table 1. Severity (number of cowbird eggs per nest) of cowbird brood parasitism experienced by Prothonotary Warblers breeding on study sites in the Cache River watershed in southern Illinois, 1994-1999. Values are derived only from nest boxes with 44-mm openings so that accessibility to nests by cowbirds is constant among all sites.

Site	Year					
	1994	1995	1996	1997	1998	1999
Buttonland Swamp (BS, WV, EP)	1.00 (9)*	1.53 (19)	2.67 (30)	1.49 (39)	2.80 (29)	2.00 (21)
Limekiln Slough (LS)	1.00 (5)	0.43 (7)	1.57 (7)	1.33 (9)	1.75 (4)	1.75 (4)
Hickory Bottoms (HB)	0.40 (5)	1.71 (7)	2.00 (2)	1.50 (2)	1.50 (4)	0.33 (3)
Main Tract (MTN, MTS)	0.58 (12)	0.76 (17)	0.73 (26)	0.74 (23)	1.43 (7)	0.42 (12)
Porter's Bottoms (PBN, PBS)	----	----	----	1.05 (38)	1.32 (53)	1.13 (31)
Add's Branch Corridor (ABC)	1.14 (7)	0.75 (4)	0.69 (13)	0.53 (36)	0.81 (36)	0.48 (25)
Heron Pond (HP)**	----	----	----	1.19 (21)	2.20 (25)	1.88 (26)
Cache River (CR)**	0.00 (3)	0.80 (5)	0.60 (15)	0.54 (37)	1.04 (24)	1.13 (16)
Cottonmouth (CM)**	0.00 (2)	0.14 (7)	0.33 (9)	0.24 (21)	0.74 (19)	0.09 (11)
Scott Robinson (SR)**	----	----	----	0.00 (10)	0.57 (14)	0.33 (9)
Watson's Pond (WP)**	0.00 (2)	0.71 (17)	0.70 (20)	0.83 (18)	0.53 (19)	1.00 (8)
Cypress Pond (CP)**	----	----	----	0.47 (17)	0.38 (16)	0.56 (16)
Forman Tract South (FTS)***	----	----	----	----	----	1.00 (9)
Old Cache River Slough (OCRS)***	----	----	----	----	----	0.83 (6)
Rose Farm (RFC, RFS)***	----	----	----	----	----	0.94 (17)
Plantation Forest (PF)***	----	----	----	----	----	1.20 (5)
Little Grassy Slough (LGS)***	----	----	----	----	----	1.30 (10)
Total (all sites combined)	0.69 (45)	0.93 (83)	1.22 (122)	0.82 (271)	1.28 (250)	1.04 (229)

* (n) = number of nests used to calculate values. Only those nests with complete clutches were used for these calculations.

** Sites are all within the vast area of floodplain and swamp forest within the Heron Pond/Little Black Slough State Natural Area. The HP study site is located near the south/southeast edge of the natural area where it is bordered by a large cattle farm.

*** Sites are adjacent to the Grassy Slough Preserve (formerly Rose Farm) that was farmed for the last time in 1999.

Table 2. Productivity (host young/color-marked female/breeding season) experienced by Prothonotary Warblers breeding on study sites in the Cache River watershed in southern Illinois, 1995-1999. These values need to be **greater than 1.70** for a site to be classified as a **source** given an adult survival rate of **70%** and a juvenile survival rate of **35%**.

	Year				
Site	1995	1996	1997	1998	1999
MTN	**2.90** (20)*	**1.90** (22)	0.70 (15)	0.90 (9)	0.00 (8)
HB	**2.90** (7)	0.60 (5)	1.20 (6)	0.30 (7)	0.00 (--)
CM	1.60 (7)	1.20 (9)	0.50 (6)	0.00 (5)	0.67 (6)
WP	**2.40** (36)	0.20 (36)	0.45 (25)	0.20 (24)	0.80 (5)
ABC	0.70 (10)	0.00 (6)	1.10 (8)	0.00 (10)	0.00 (5)
MTS	**4.50** (12)	**2.70** (10)	0.50 (11)	1.50 (2)	0.80 (5)
BS	**3.50** (20)	**3.70** (36)	**2.20** (44)	**3.30** (47)	**2.40** (35)
CR	**3.50** (4)	1.53 (19)	1.00 (10)	**1.75** (4)	1.43 (7)
LS	**3.30** (12)	1.20 (11)	**1.80** (12)	0.50 (10)	0.57 (7)
PBSW	0.40 (12)	-----	-----	-----	-----
PBS	-----	-----	0.50 (6)	**3.80** (8)	0.60 (5)
PBN	-----	-----	0.60 (7)	1.60 (8)	**2.00** (5)
SR	-----	-----	1.30 (4)	**2.50** (4)	**2.60** (5)
CP	-----	-----	1.40 (5)	0.80 (6)	0.86 (7)
HP	-----	-----	0.00 (5)	0.40 (11)	1.45 (11)
PBW	-----	-----	-----	-----	**4.17** (6)
PBSE	-----	-----	-----	-----	**4.00** (5)
MTE	-----	-----	-----	-----	**5.50** (4)
MTW	-----	-----	-----	-----	**2.50** (6)
FTS	-----	-----	-----	-----	**2.00** (2)
OCRS	-----	-----	-----	-----	1.25 (4)
RF	-----	-----	-----	-----	**3.91** (11)
PF	-----	-----	-----	-----	0.75 (4)
LGS	-----	-----	-----	-----	**2.80** (5)
TOTAL	**2.61** (140)	**1.72** (154)	1.19 (164)	1.59 (155)	**1.96** (158)
% SITES THAT ARE SOURCES	70% (10)**	33% (9)	14% (14)	21% (14)	43% (23)

* (n) = number of color-marked females on that site in that year.
** (n) = total number of study sites in that year.

Table 3. Age structure of the adult Prothonotary Warblers breeding on study sites in the Cache River watershed in southern Illinois, 1999.

Age*	Percentage of Population	
	Female (n=182)	Male (n=153)
SY	**13**	**36**
ASY	**34**	**22**
TY	**14**	**10**
ATY	**19**	**10**
FoY	**8**	**6**
AFoY	**6**	**7**
FiY	**0.5**	**5**
AFiY	**4**	**2.5**
SiY	**----**	**0.5**
ASiY	**1.5**	**0.5**
SeY	**----**	**0.5**

* The age of individuals that are new to study sites (unbanded) is classified either as SY or ASY based on plumage and morphological characteristics (wing, tail, and tarsus length). If an SY bird returns the following year it then becomes a TY, if an ASY returns the next year it becomes an ATY, etc.