





January 12, 1999

Please find enclosed a final report for the 1998 field season for the Prothonotary Warbler/flooplain forest restoration research project being conducted in the Cache River watershed in southern Illinois. Thank you for your continuing support of this groundbreaking, comprehensive, important long-term research connecting avian biology to restoration ecology and monitoring the success of the restoration effort in the Cache River watershed (including the Cypress Creek NWR, the Cache River SNA, the Heron Pond/Little Black Slough Nature Preserve, and Limekiln Springs Preserve).

Sincerely,

Affry P. Hoovy

Jeffrey P. Hoover Graduate Research and Teaching Assistant Illinois Natural History Survey 607 E. Peabody Drive Champaign, IL 61820 (217) 244-2174 e-mail: j-hoover@staff.uiuc.edu Final Report to:

Illinois Nature Preserves Commission

The Influence of Hydrology and Nest Predation on the Site Fidelity and Population Dynamics of a Neotropical Migratory Bird: Implications for Floodplain Restoration

1 March 1998 to 1 September 1998

by:

Jeff Hoover and Scott Robinson Illinois Natural History Survey 607 E. Peabody Drive Champaign, IL 61820

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During the 1998 field season, we continued to monitor the nesting success of over 200 pairs of color-marked Prothonotary Warblers (Protonotaria citrea) nesting among the now 20 study sites within the Cypress Creek NWR and Cache River Wetlands. Prothonotary Warblers used over 550 nest boxes (of the 1,200 available). We recorded the fate of each nesting attempt as well as the water depth beneath each nest box at 4-day intervals from 15 April to 15 August. We captured and color-marked (or identified those returning from previous years) nearly all individual warblers nesting on the study sites. We monitored all active nests until they were either preyed on, abandoned, or resulted in young fledging from the nest. We determined the identity of the nest predators responsible for nest predation events based on signs left at the nest box (tracks, condition of nest box and nest, condition of nest contents, etc.). We placed an aluminum USFWS band on all young that fledged from nests. We also continued two experiments including: 1) an experiment studying the selection of nest boxes that were placed at different heights on the same tree to determine any preferences by female Prothonotary Warblers and to compare their choices to the hydrology (water-level fluctuations) for that particular site; and 2) an experiment to test the "decision rules" hypothesis which states that between-year site and territory fidelity of individuals are based on experience-based choices (based on nesting success) made by birds and not simply the result of differential mortality. We also conducted censuses on all of the study sites.

We recorded nesting information for 556 Prothonotary Warbler nests in nest boxes, and for 12 nests in natural cavities among the 20 study sites. We color-marked approximately 340 individual adult warblers (approx. 210 females and 130 males), and followed their nesting activity throughout the entire breeding season. We are now able to accurately determine the age structure of the population in the watershed each year because of the previous years of banding adult and juvenile warblers (Table 1). This age structure can be compared from year to year in an attempt to understand how weather, water levels,

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nesting success, habitat restoration, and interactions of these factors may influence the age structure over time.

The study sites, for a second year in a row, received less rainfall than the summers of 1995-1996. A consequence of this was a second consecutive year with a general decrease in water depth beneath the nest boxes. As a result of this, the nest predation rates were higher than they had been in previous years. Raccoons (Procyon lotor) were the primary nest predator responsible for nesting failure for Prothonotary Warblers and accounted for approximately 70-80% of all nest predation events (Figure 1). The remaining 20-30% of nest predation events were caused by Black Rat (Elaphe obsoleta obsoleta) and Speckled King (Lampropeltis getulus holbrooki) Snakes, Southern Flying Squirrels (Glaucomys volans), and rarely by avian nest predators such as Common Grackles (Quiscalus quiscula). Nest predation by Mink (Mustela vison) has not been present since the summer of 1995. This pattern of nest predation events is similar to that observed during the 1994-1997 breeding seasons (with the exception of the small component of nest predation by Mink in 1995).

Rates of nest predation in 1998 were compared among six water depth categories (Fig. 2). Two new categories were added this year. The 0-10 category used in previous years was split into three categories including a natural levee category (the raised area of land along the Cache River that rarely has standing water on it and has structural complexity of vegetation), a 0-cm (zero) category (exposed mudflats where water has drawn down to nothing), and a 1-10-cm category for the areas with very shallow water present. As stated above, due to it being a relatively dryer summer, rates of nest predation were higher overall. An exception to this was the deep water category which has had low (< 0.03) rates of nest predation every year of this study. For areas where water was present, the general pattern observed in previous years held, and rates of nest predation decreased as the depth of water beneath nests increased in 1998 (Figure 2).

Rates of nest predation decreased substantially when the depth of water beneath nests was >30 cm. An interesting pattern has emerged, however, with the splitting of the 0-10-cm category. The natural levee nests, even though water depth beneath them is almost always 0 cm, had a moderate rate of nest predation that was substantially less than the 0-cm or 1-10-cm categories and similar to the boxes with a moderate depth of water beneath them (11-20-cm and 21-30-cm categories). These rates are, however, still significantly higher than those nests in deep (>30 cm) water. This result is interesting as it is an apparent exception to the "no- or very shallow-water equals the highest rates of nest predation" rule that has previously been suggested by our results. The pattern for daily predation rates is almost entirely driven by patterns of nest predation by Raccoons (Fig. 3). The results from research this summer continue to suggest that Raccoons spend more time foraging in shallow water (< 30 cm) or exposed mudflats than they do in deep water. Following a pulse of water input on a study site, as wet forests and swamps began to dry up, foraging by Raccoons became more concentrated along the edges of and in the diminishing areas of water. While foraging in this manner, Raccoons came into contact with more and more Prothonotary Warbler nests as they foraged for crayfish and other food items and they then incidentally preved on the active nests following the decrease in water depth beneath the nest boxes. It is possible that the increased ground- and shrubcover present on the natural levees along the river hinder the ability of Raccoons to find the nests, or it is possible that Raccoons spend less time foraging on the natural levees and more time along the interface of the water and dry ground that is present in the backwater and swamp areas located some distance away from the river. We will pursue these issues further with future research.

Each nest was vulnerable to predation for the entire time that it was active (from the beginning of nest building to the fledging of young). As a consequence of this, a reasonable estimate for the duration of water >30 cm that would be necessary to increase nesting success for an entire study site would be a minimum of 50-60 days because not all

of the individual birds began nesting at the same time, and because water level fluctuations and nesting were not necessarily linked. Based on the data that we now have, Prothonotary Warblers preferred to nest over water, but they did not have a preference for (or were unable to determine) a particular water depth. These results suggest that the birds are attracted to areas that have shallow or deep water, with the result being high levels of nest predation for those nesting over shallow water.

At the other extreme, too much water can also decrease nesting success by flooding active nests. The dryer breeding season this year limited the flooding to just two nests in the Limekiln Slough study site (see Fig. 11). This site receives runoff from over 2,000 acres of adjacent agricultural land and in wetter years receives several spike floods during a single breeding season (see Figs. 11a-d). In previous years (especially 1995-1997), several active Prothonotary Warbler nests (on several different study sites) in the Cache River watershed were flooded. In light of this, the experiment to determine preference for nest height by Prothonotary Warblers, in relation to water level fluctuations, vielded some interesting results. In general, the Prothonotary Warblers had no particular preference for nest height prior to flood events (first nesting attempts only), and 37%, 21%, and 42% of the 24 pairs of warblers chose low, medium, and high boxes, respectively. This suggests that the warblers are unable to "anticipate" a flooding event and do not choose the highest available nest boxes, even in flood-prone areas. The warblers did, however, move to the high nest boxes if a flood event occurred. This result suggests that the birds are able to adapt to highly variable water levels in the short-term. As we continue our research by following individually color-marked birds over several breeding seasons, we will further explore the question of long-term adaptive responses to water-level fluctuations, especially for those individuals who have a nest flooded one year and return to the site the following year.

In 1998, hydrographs were created for each of the study sites (Figs. 4-16) based on the nest boxes with the deepest (maximum) and shallowest (minimum) water beneath them

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on each site. On a given site, all other nest boxes lie between the deep and shallow nest box water depth lines. Dashed lines are drawn at 30 cm (below which rates of nest predation become very high) and at the depth where a nest box would be flooded (usually 160-180 cm depending on the study site). The period of time during the breeding season when there are active Prothonotary Warbler nests is from the very end of April to early August. The actual productivity for each study site is given above the graph and is the average number of young produced by the color-marked females on the site for the entire breeding season. Study sites where a substantial amount of the area between the deep and shallow lines is <u>not</u> above the 30-cm line for fairly <u>long</u> durations experience very low amounts of productivity by the warblers (see Figs. 6, 7, 8, 9, 11, 15, and 16). This result is driven by the water-depth/nest-predation pattern described above.

There are also examples of sites with relatively deep water for longer durations resulting in higher levels of productivity (Figs. 10, 12, and 13). The Buttonland Swamp study site has consistently deep water each year and has had relatively high levels of productivity every year that this study has been conducted. As with most patterns in nature, there are exceptions. The study sites Main Tract North and Main Tract South (Figs. 4 and 5) have hydropatterns that should result in levels of productivity that are higher than what actually occurred there. These two sites (which are connected to each other) have a substantial population of flying squirrels on them resulting in high levels of nest predation (and lower nesting success) even though the water is relatively deep. Patterns of nest predation by flying squirrels are unrelated to water depth, thus causing this result. Another site, Scott Robinson (Fig. 14), had higher productivity than what would be expected based on the hydrograph likely because many of the nest boxes on this site were located on natural levee habitat, where rates of nest predation can be moderate to low.

Nest predation is the primary factor limiting nesting success for Prothonotary Warblers. However, because the warblers have a relatively long nesting season, can renest several times following nest predation (up to 8; J. Hoover unpubl. data), and can raise up

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to 3 broods of young in a single breeding season, individual pairs of warblers can often raise one or two broods of young and also experience a number of nest predation events. It is then important to determine how the resulting nesting success, as mediated by nest predation which is affected by depth and duration of water, influences the patterns of between-year site fidelity and territory fidelity for individual Prothonotary Warblers. The correlative (non-experimental) pattern, as well as the results of a novel experiment, have provided some intriguing results.

Individuals on experimental sites were randomly assigned the number of broods they would ultimately produce (0, 1, or 2), and their nest boxes were made Raccoon-proof so that they would produce the desired number of broods. The experiment was conducted on sites where shallow water was prevalent and rates of nest predation were high. These sites, as a consequence of the experiment, produced more young than they would had the experiment not been done. The between-year site fidelity of individual color-marked females (returning to the same study site in 1998 after nesting on the site in 1997) increased with increasing nesting success (number of broods produced in 1997) with nearly identical results for experimental and non-experimental individuals (Fig. 17). The male warblers (both experimental and non-experimental) followed a pattern identical to that of the females (increased site fidelity with increased nesting success), but differed within the unsuccessful male category between the experimental and non-experimental individuals (Fig. 18). This difference may be explained by a "neighborhood" effect where unsuccessful males may return to a site (but not necessarily to the same territory) if their neighbors are successful at producing young.

An artifact of the experimental manipulation was that there were several unsuccessful males adjacent to territories where young were successfully produced on the experimental sites. A significantly higher percentage of unsuccessful males <u>with</u> successful neighbors returned compared to unsuccessful males <u>without</u> a successful neighbor (Fig. 21). This result implies that these males are surveying adjacent territories for nesting

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success and/or are getting extra-pair copulations with neighboring females (with the result being that some of the young on neighboring territories may belong to the "unsuccessful" male. An analysis of paternity is necessary to determine this, and we are planning to include this in the continuing research within the Cache River watershed.

Considering only those individuals that returned to study sites between years, we compared fidelity to territories for those producing 0, 1, or 2 broods of young. The patterns of territory fidelity were similar to those for site fidelity and increased with increasing nesting success for both experimental and non-experimental males and females (Figs. 19 and 20). This indicates that even if an unsuccessful individual returns to a site, they will usually move to a new territory. These results, for both between-year site and territory fidelity, support the "decision rules" hypothesis which states that individuals return to sites and territories as a result of choices that are made based on previous experience. The choices are whether or not to return to a site the following year and then, upon returning, whether or not to use the same territory. The experience is the breeding season, and the decision appears to be based on the number of broods produced during it.

With the above information, we are now piecing together several components of the floodplain forest ecosystem (Fig. 22). We are improving out understanding of how weather, adjacent land use, and to a lesser extent beavers, influence fluctuation of water levels within the Cache River watershed. These fluctuations of water levels can indirectly affect nesting success of Prothonotary Warblers by influencing the patterns of movements made by Raccoons, in turn influencing rates of nest predation. Fluctuations of water levels can also directly affect nesting success (although to a lesser extent) by flooding nests during "spike" floods. The nesting success then influences both between-year site and territory fidelity and ultimately the population dynamics on individual sites and at larger scales (watershed, region, etc.).

Sites with relatively high productivity (e.g. Buttonland Swamp) have relatively high returns of individuals between years, and these sites have stable numbers of pairs breeding

on them from year to year. We are now starting to see, however, how sites that suffer two consecutive years of poor productivity can have populations that crash. Main Tract North and Main Tract South together had approximately 30 pairs of birds occupying territories on them during the 1994-1997 breeding seasons. In 1996 and 1997, nesting success was very low on these sites and the study population dropped to just 11 pairs in 1998. These dramatic fluctuations are likely a combination of many of the adults not returning to the site because of the low nesting success (decision rules), and the resultant decrease in individuals present on the site early in the breeding season that may attract conspecifics to that site (conspecific attraction). Sites that have few returning individuals (which usually are the earliest to arrive at the beginning of the breeding season) may be less attractive to those individuals that are new to an area and are looking for habitat in which to establish a territory and attempt breeding. Sites with low nesting success likely have population crashes resulting from low returns of adults, and a diminished potential to attract new birds. With continued monitoring of these populations, their reproductive success, and subsequent returns, we will be able to better understand how population dynamics respond to changes in the many interconnected components of the floodplain forest ecosystem.

To date, nearly 1,100 Prothonotary Warbler young that have fledged from successful nests have been banded (including 250 this past year). This large number of banded fledglings has increased our ability to obtain information in subsequent years about one of the least-known aspects of avian dispersal, natal philopatry. To date, twenty-four of the 1,100 warbler young banded in nests have returned in subsequent years as breeding adults, an equal number being males and females. This low return suggests that these young are dispersing long distances and/or mortality rates are high prior to their first breeding season. With each additional year and the return of more young, we will be able to begin relating returns of young to whether they were born in the early or later part of the breeding season, and to whether or not they had to compete with cowbird nestmates as nestlings and fledglings.

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The depth of water has no influence on the amount of brood parasitism by Brownheaded cowbirds. Brood parasitism is more a function of landscape composition. Brood parasitism was prevalent in all areas within the watershed, but levels were lowest in the largest, most unfragmented portion of the restoration area (Heron Pond/Little Black Slough) (Table 2). There was, however, a strong edge-related effect within this large area of habitat and the nest boxes closest to the south/southeast edge (HP), which is bordered by a large cattle farm, experienced relatively high levels of brood parasitism. This large block of habitat likely has lower rates of brood parasitism (in general) because it has a relatively higher abundance of cowbird hosts nesting in it. Parasitism by the cowbirds is then diluted (fewer cowbird eggs per host nest) among the larger number of hosts relative to some of the smaller patches of floodplain forest where hosts are less abundant. These results suggest the importance of adding on to the medium and larger tracts and consolidating existing smaller tracts of floodplain forest. As restoration proceeds and the landscape becomes less hospitable for cowbirds and more suitable for neotropical migratory birds, by continuing to study a single species (the Prothonotary Warbler) we will be able to document the expected reduction in brood parasitism.

1. A.

Restating the conclusions of this report:

- During the 1998 field season, we monitored over 1,200 nest boxes placed among 20 sites in the Cache River Wetlands and Cypress Creek NWR. Over 550 nest boxes were used by Prothonotary Warblers. Approximately 200 pairs of adult warblers were individually color-marked, and 250 fledgling warblers were marked with aluminum bands.
- Raccoons were again responsible for the majority of nest predation events for Prothonotary Warbler nests.
- Rates of nest predation decreased as the depth of water beneath nests increased. In general, the rate of nest predation was highest for nests over mudflats or over water 1-10 cm deep, intermediate for nests on natural levees or over water 11-20 cm deep, and consistently low for nests in water deeper than 30 cm.
- The patterns of nest predation that we observed for Prothonotary Warblers are a consequence of the activity patterns of Raccoons being influenced by hydrologic fluctuations during the breeding season.
- During the breeding season, a minimum 34-day duration of water deeper than 30 cm would increase the success of individual nests and a duration of 50-60 days would increase the success of many nests within a particular site. An exception to this would be for sites such as Main Tract North and South where there was a local effect of nest predation by flying squirrels that was independent of the depth of water beneath nest boxes.
- Fluctuations in water levels affect rates of nest predation, in turn influencing nesting success. Nesting success (number of broods produced in a breeding season) influences both the between-year site and territory fidelity of individual Prothonotary Warblers. Site fidelity of females and males increases with increasing numbers of broods produced. For those individuals returning to sites, territory fidelity also

increases with increasing numbers of broods produced. Between-year site and territory fidelity influence population dynamics directly based on the number of individuals returning, and possibly indirectly through conspecific attraction. (See Fig. 22)

- "Spike" floods do directly cause nesting failure, but there was no predisposition for Prothonotary Warblers to use the highest available nest box when given the choice.
 Following a flood event, individuals did respond adaptively in the short term and used the highest available nest boxes. Continuing research will yield information on any long-term modifications of these behaviors regarding nest selection.
- Brood parasitism was prevalent in all areas within the watershed, but levels were lowest in the largest, most unfragmented portion of the restoration area (Heron Pond/Little Black Slough).

Figure Legends

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Figure 1. Nest predators responsible for nest predation events for Prothonotary Warblers nesting in boxes in the Cache River Wetlands and Cypress Creek NWR (1998).

Figure 2. Daily predation rates compared among six water-depth related categories for Prothonotary Warbler nest boxes in the Cache River Wetlands and Cypress Creek NWR (1998).

Figure 3. Nest predators responsible for nest predation events for six water-depth related categories for Prothonotary Warblers nesting in boxes in the Cache River Wetlands and Cypress Creek NWR (1998).

Figures 4-16. Hydrographs study sites in the Cache River Wetlands and Cypress Creek NWR (1998). Maximum and minimum lines represent the nest boxes with the deepest and shallowest water beneath them, respectively, on each site. On a given site, all other nest boxes lie between the maximum and minimum nest box water depth lines. Dashed lines are drawn at 30 cm (below which rates of nest predation become very high) and at the depth where a nest box would be flooded (usually 160-180 cm depending on the study site). The period of time during the breeding season when there are active Prothonotary Warbler nests is from the very end of April to early August. The actual productivity for each study site is given above the graph and is the average number of young produced by the color-marked females (n) on the site for the entire breeding season.

Figures 11a-d. Hydrographs for Limekiln Slough for 1995-1998 illustrating the annual variation in the amount and frequency of water level fluctuations.

Figure 17. A comparison of between-year site fidelity (percentage returning to sites in 1998) of experimental and non-experimental color-marked female Prothonotary Warblers that produced 0, 1, or 2 broods during the 1997 breeding season in the Cache River Wetlands and Cypress Creek NWR. Numbers above bars represent sample sizes.

Figure 18. A comparison of between-year site fidelity (percentage returning to sites in 1998) of experimental and non-experimental color-marked male Prothonotary Warblers that produced 0, 1, or 2 broods during the 1997 breeding season in the Cache River Wetlands and Cypress Creek NWR. Numbers above bars represent sample sizes.

Figure 19. A comparison of between-year territory fidelity (of those individuals returning to sites in 1998) of experimental and non-experimental color-marked female Prothonotary Warblers that produced 0, 1, or 2 broods during the 1997 breeding season in the Cache River Wetlands and Cypress Creek NWR. Numbers above bars represent sample sizes.

Figure 20. A comparison of between-year territory fidelity (of those individuals returning to sites in 1998) of experimental and non-experimental color-marked male Prothonotary Warblers that produced 0, 1, or 2 broods during the 1997 breeding season in the Cache River Wetlands and Cypress Creek NWR. Numbers above bars represent sample sizes.

Figure 21. A comparison of between-year site fidelity (percentage returning to sites in 1998) of unsuccessful color-marked male Prothonotary Warblers that either did or did not have a successful neighbor during the 1997 breeding season in the Cache River Wetlands and Cypress Creek NWR. Numbers above bars represent sample sizes.

Figure 22. A diagram of the interconnections of some of the components of the floodplain forest ecosystem in the Cache River wetlands pertinent to Prothonotary Warblers.

Table 1. Age structure of the adult Prothonotary Warblers breeding on study sites in theCache River watershed in southern Illinois, 1998.

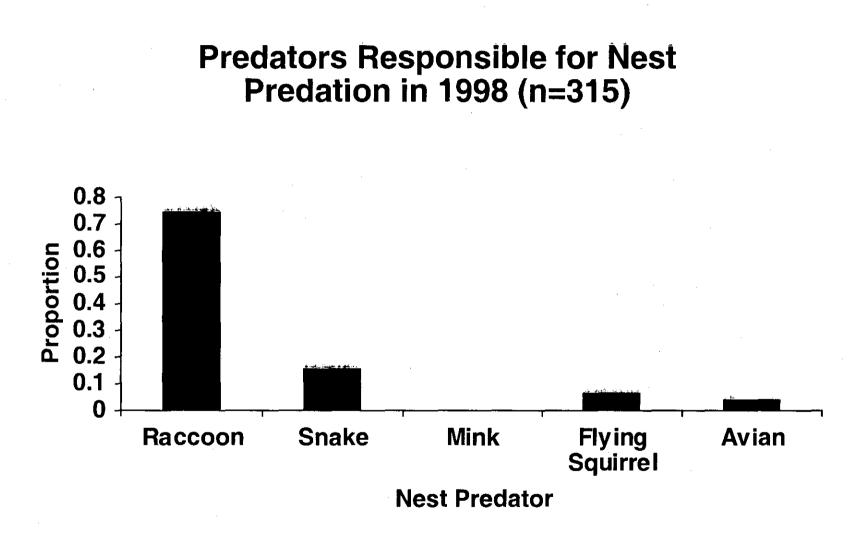
Age*	Year Born	n (percent of total)
SY (Second Year)	1997	76 (22%)
ASY (After Second Year)	Before 1997	107 (32%)
ΓY (Third Year)	1996	54 (16%)
ATY (After Third Year)	Before 1996	53 (16%)
FoY (Fourth Year)	1995	14 (4%)
AFoY (After Fourth Year)	Before 1995	22 (7%)
FiY (Fifth Year)	1994	3 (1%)
AFiY (After Fifth Year)	Before 1994	7 (2%)
SiY (Sixth Year)	1993	1 (0.2%)
ASiY (After Sixth Year)	Before 1993	1 (0.2%)

* 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. Table 2. Amounts of cowbird brood parasitism experienced by adult Prothonotary Warblers breeding on study sites in the Cache River watershed in southern Illinois, 1998. These values are derived from nest boxes with a 44-mm opening size only so that accessibility to nests by cowbirds is constant among all sites.

Site	Mean no. of cowbird eggs per nest (n)*
Buttonland Swamp (BS)	2.80 (29)
Limekiln Slough (LS)	1.75 (4)
Hickory Woods (HW) (formerly known	1.50 (4)
as Kessler Tract - KT)	
Main Tract (MT)	1.43 (7)
Porter's Bottoms (PB)	1.32 (53)
Add's Branch Corridor (ABC)	0.81 (36)
Heron Pond (HP)**	2.20 (25)
Cache River (CR)**	1.04 (24)
Cottonmouth (CM)**	0.74 (19)
Scott Robinson (SR)**	0.57 (14)
Watson's Pond (WP)**	0.53 (19)
Cypress Pond (CP)**	0.38 (16)

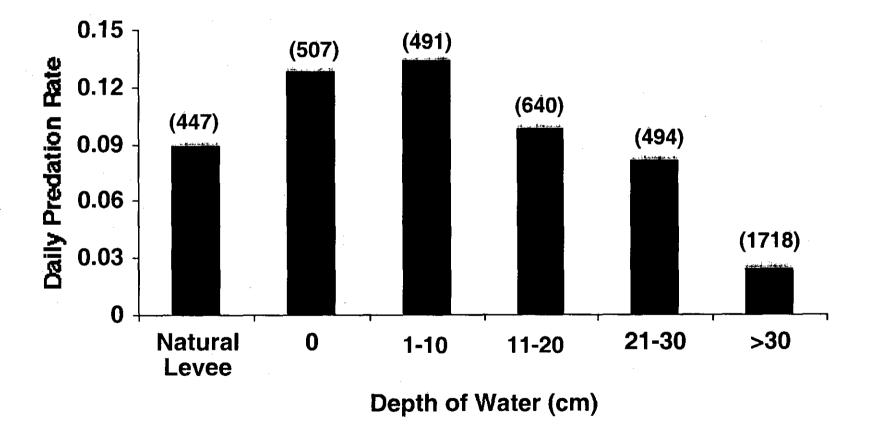
* n = number of nests used to calculate means. Only those nests with complete clutches were used for these calculations.

** 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.

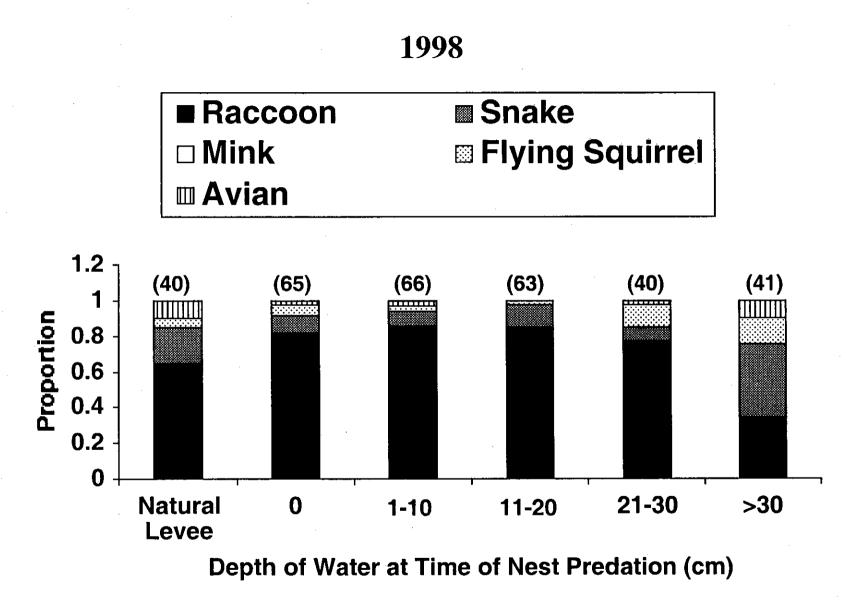




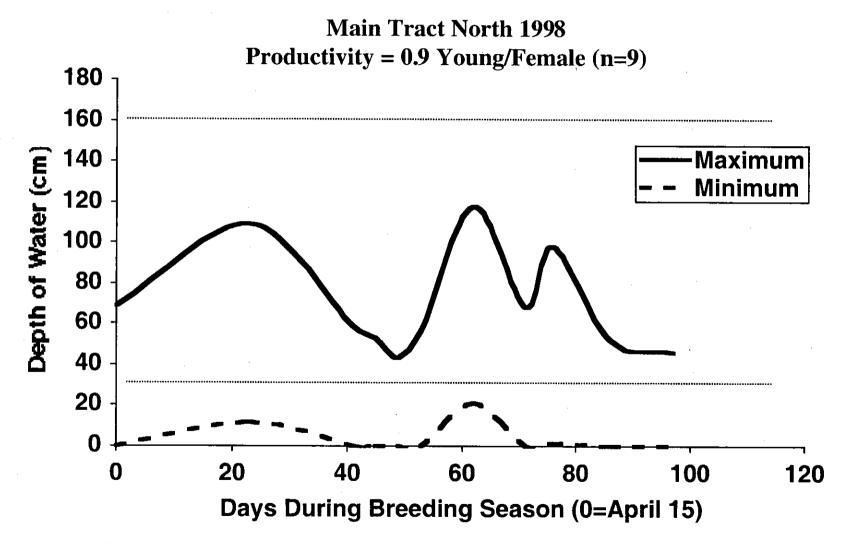
Daily Predation Rates (1998)



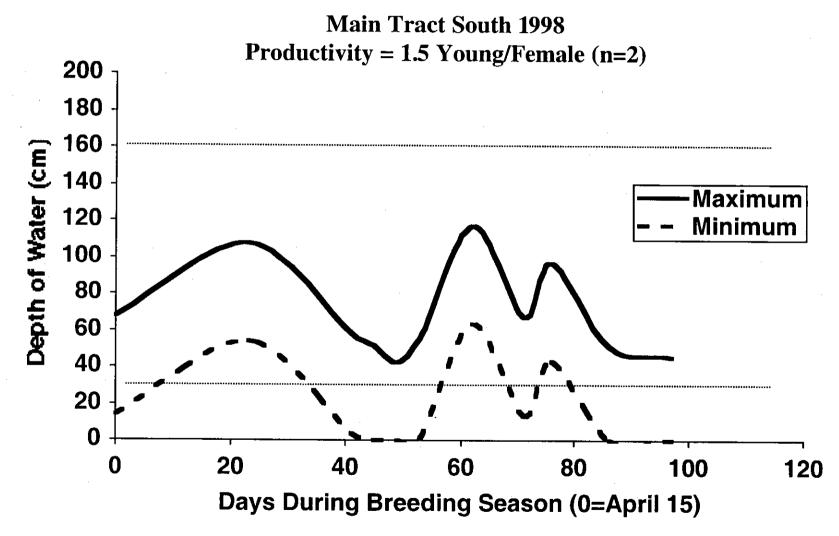






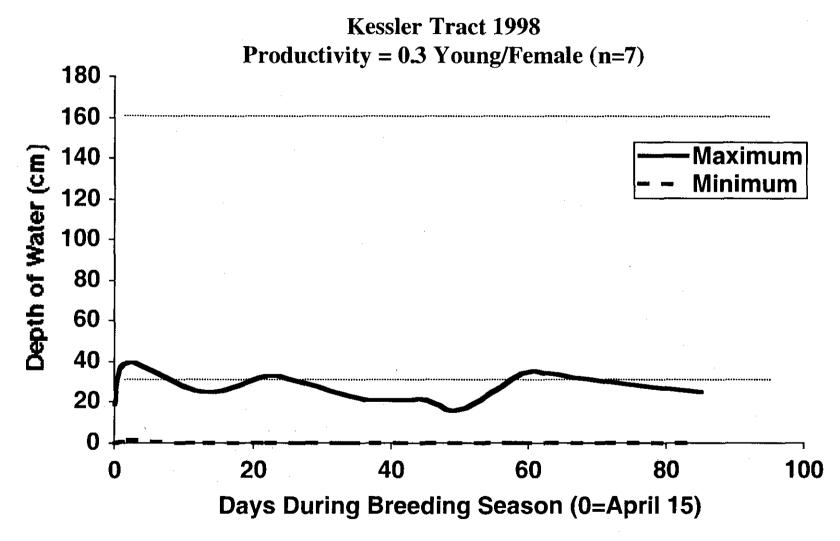








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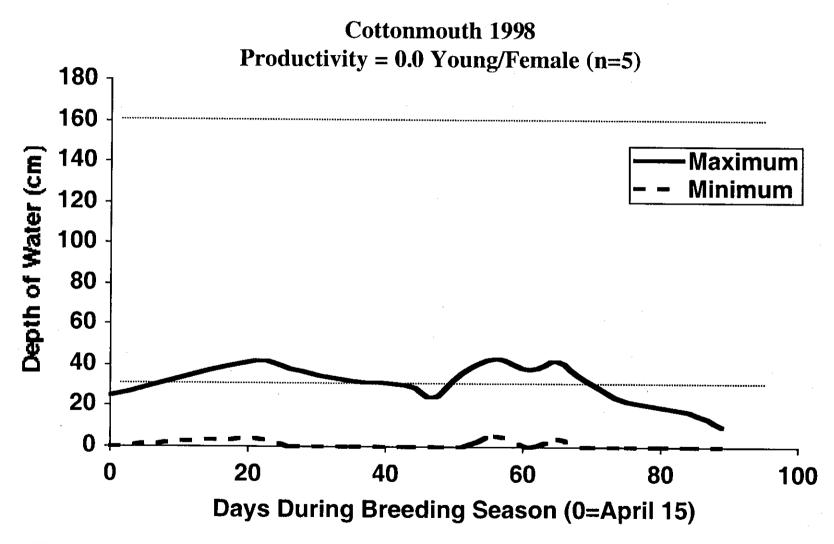


Figure 7.

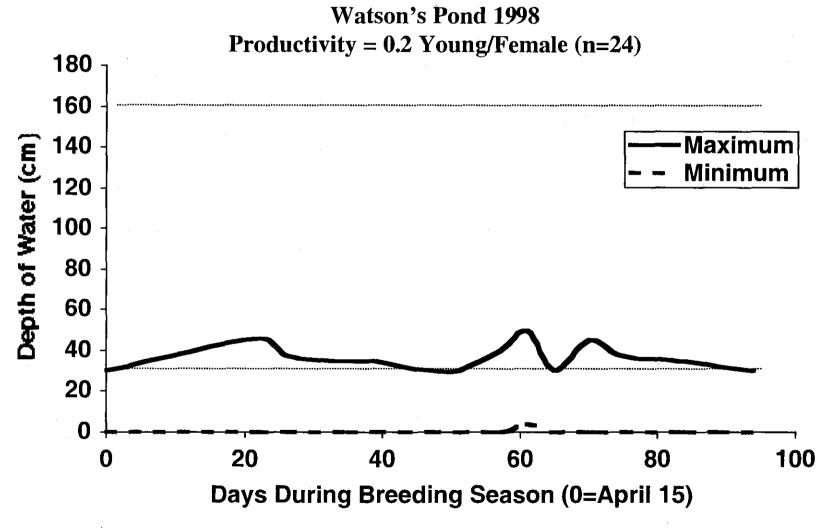
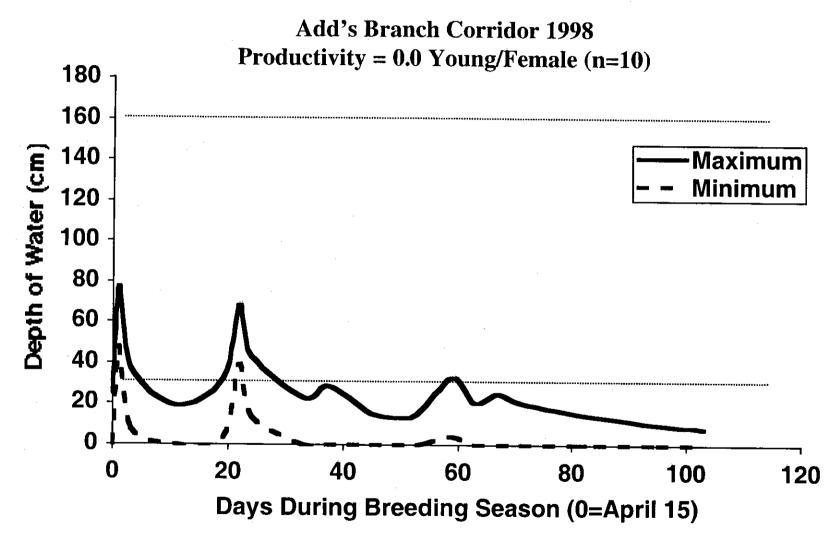
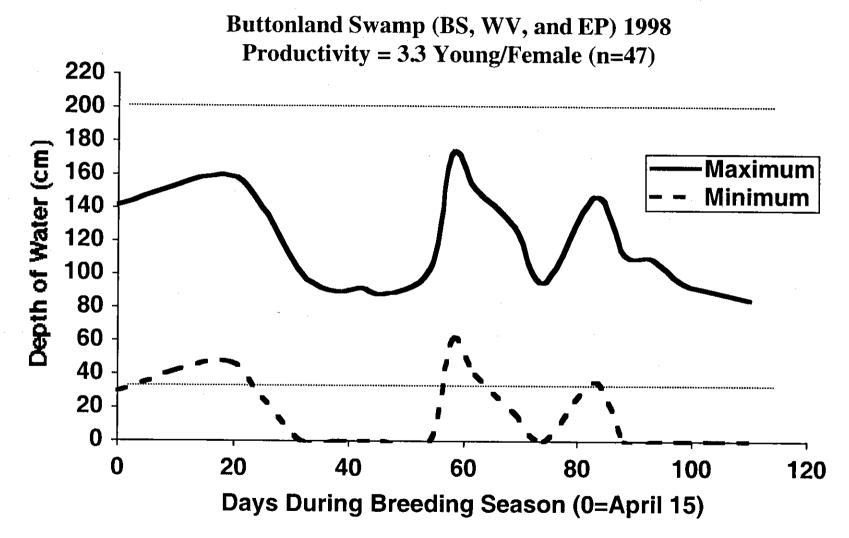


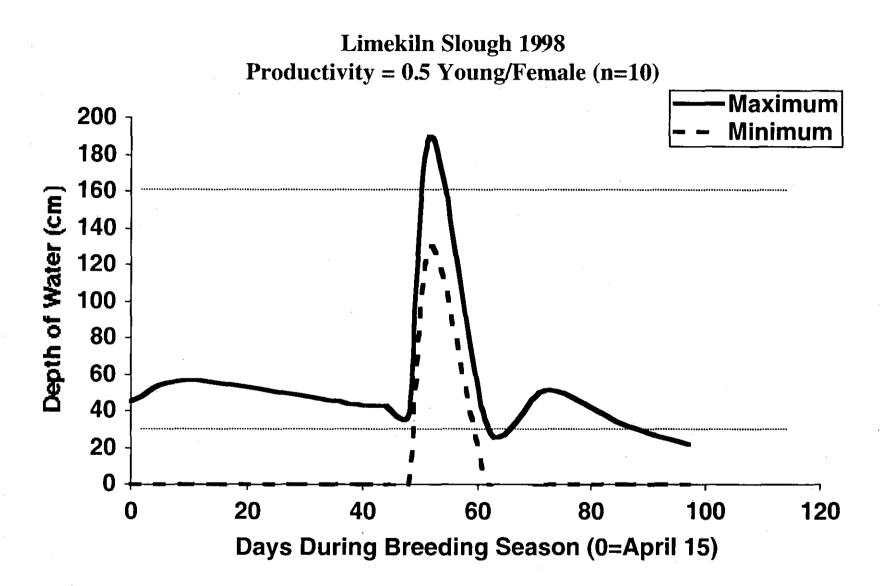
Figure 8.



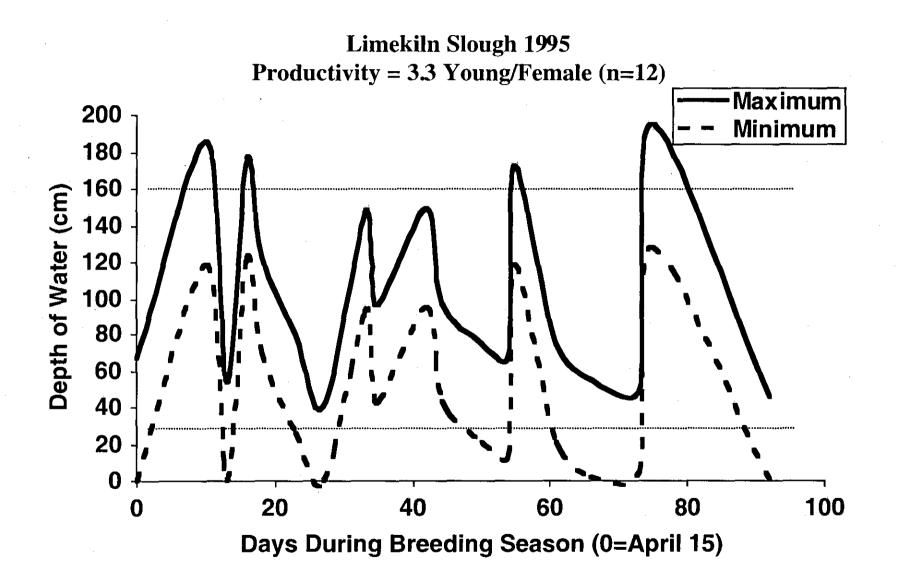




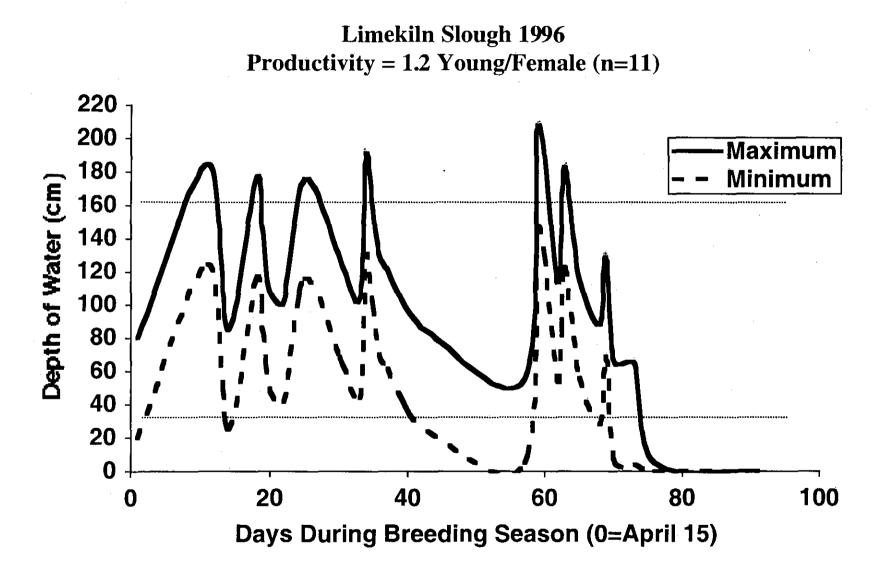




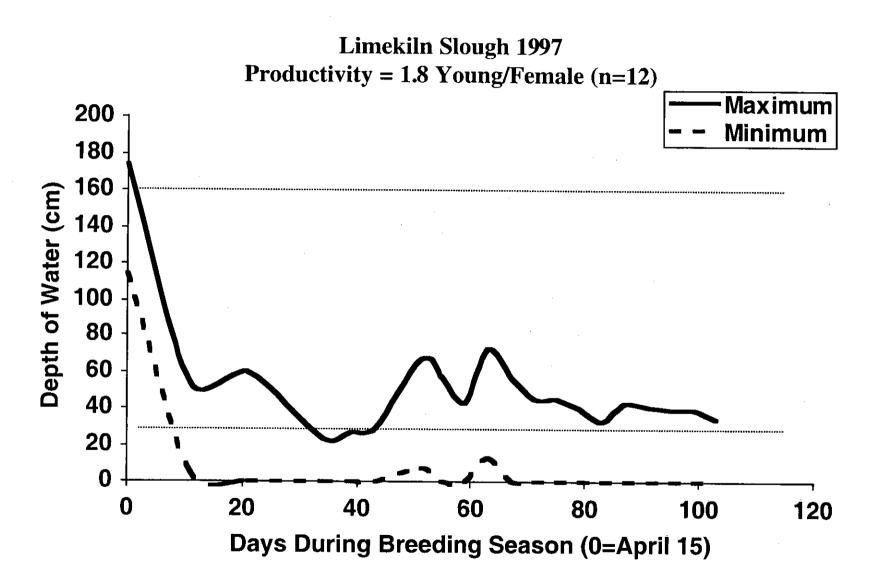




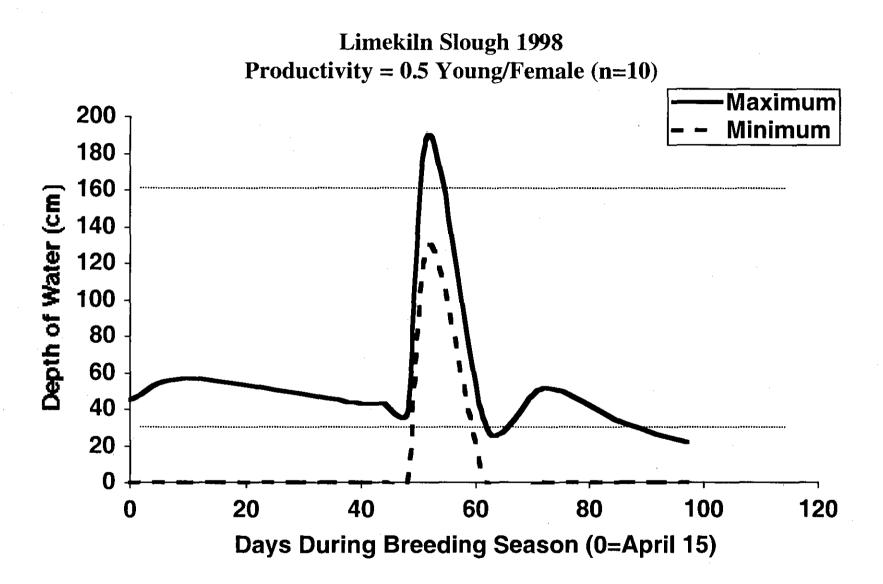




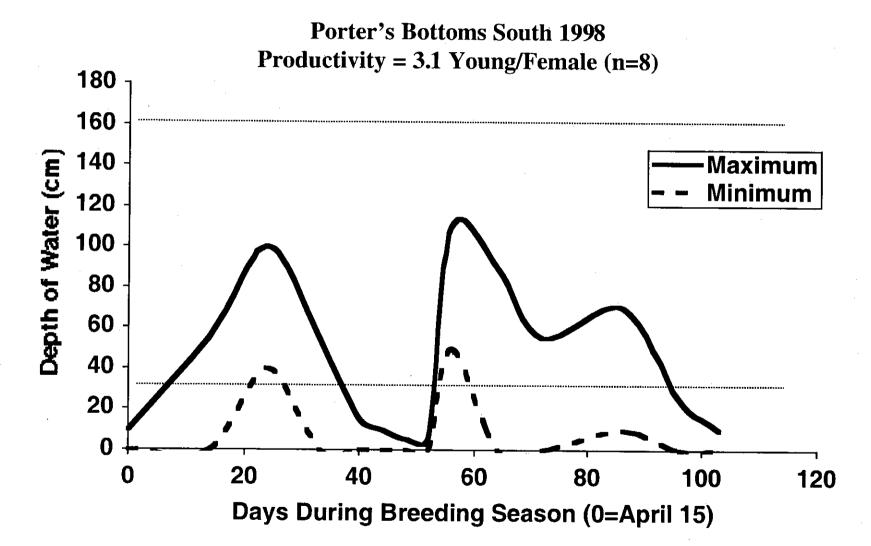




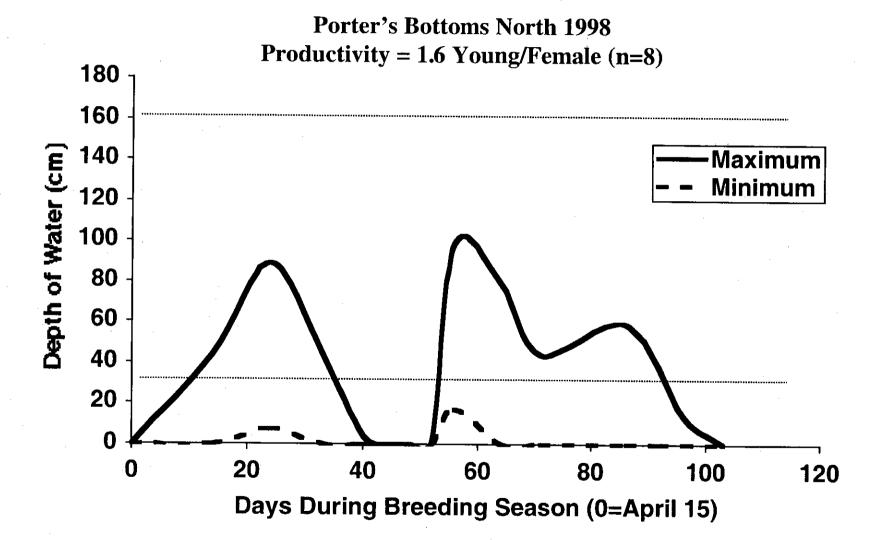




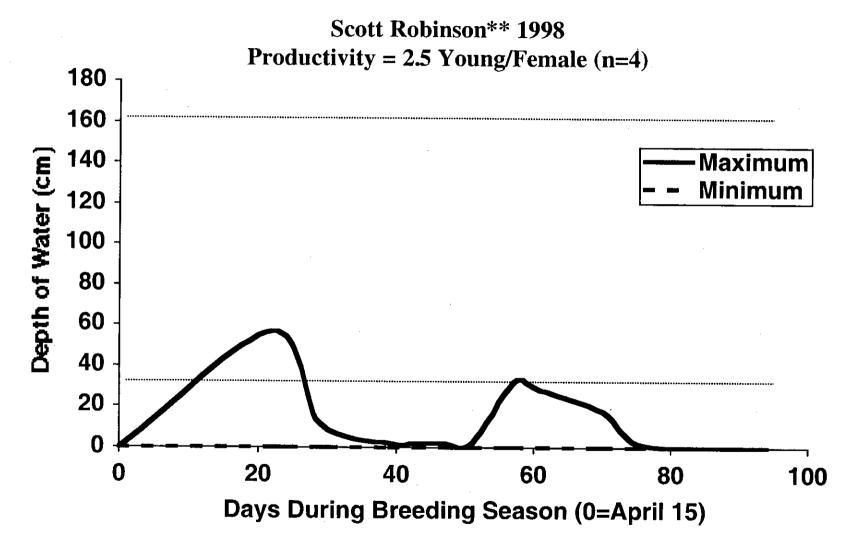




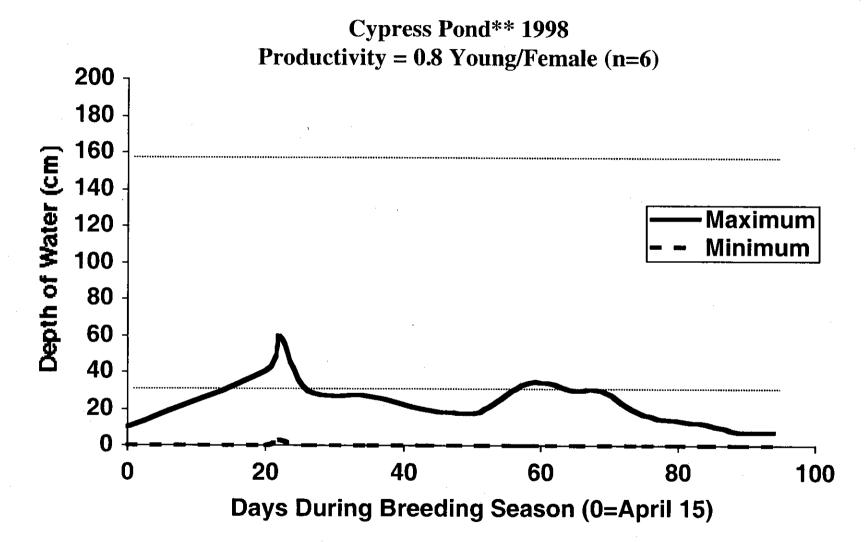


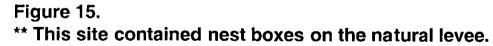




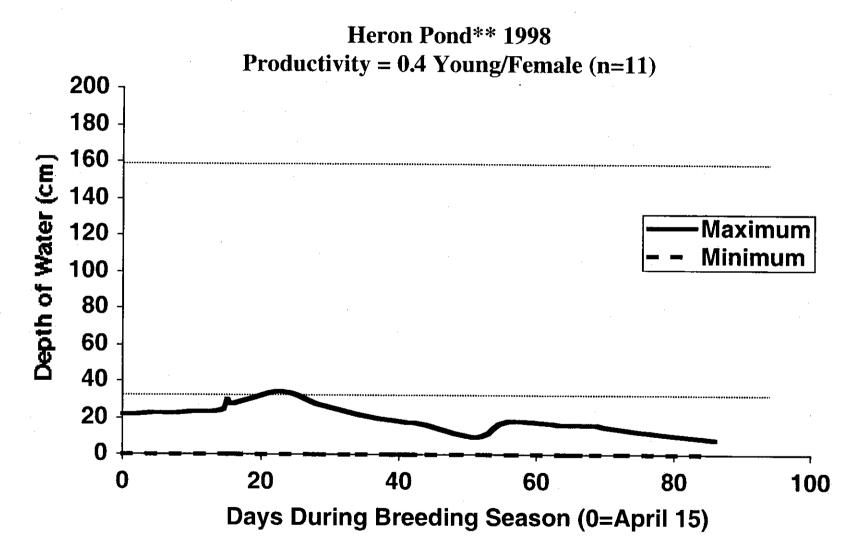


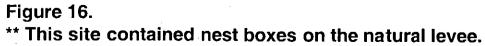






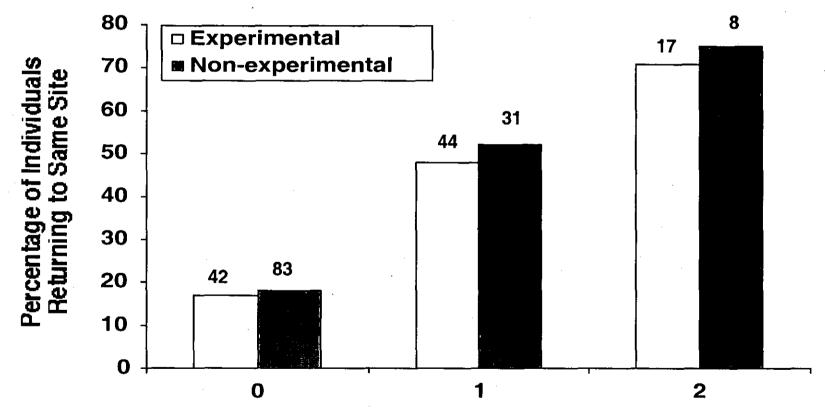






Between-Year Site Fidelity of Females

(for individuals nesting on study sites 1997-1998)

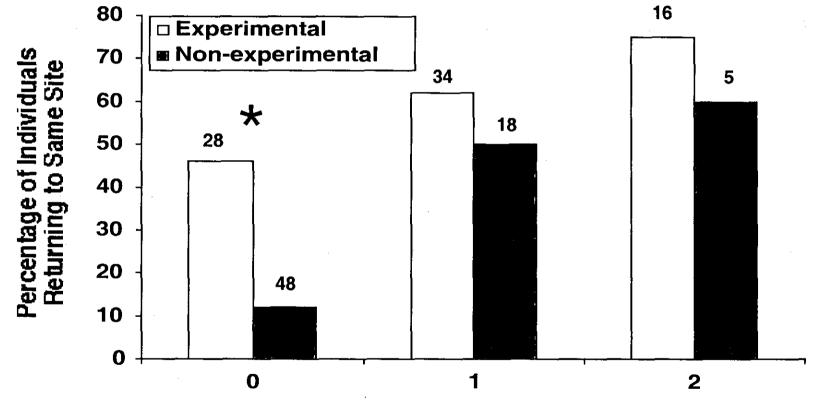


Number of Nesting Successes in Previous Year

Figure 17.

Between-Year Site Fidelity of Males

(for individuals nesting on study sites 1997-1998)

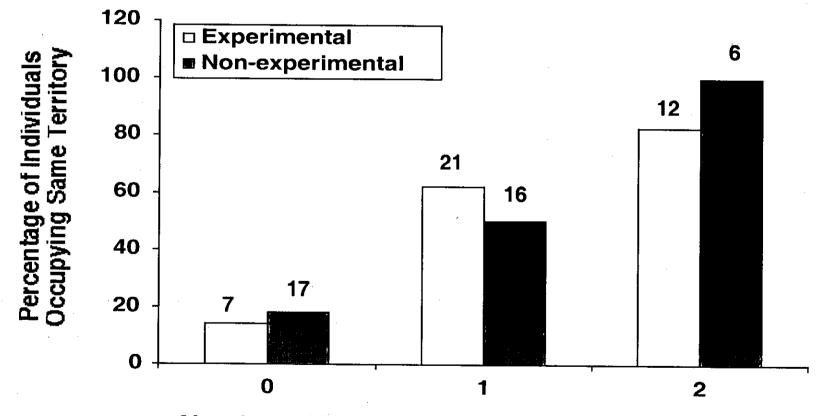


Number of Nesting Successes in Previous Year

Figure 18.

Between-Year Territory Fidelity of Females

(for individuals that returned to study sites in 1998)

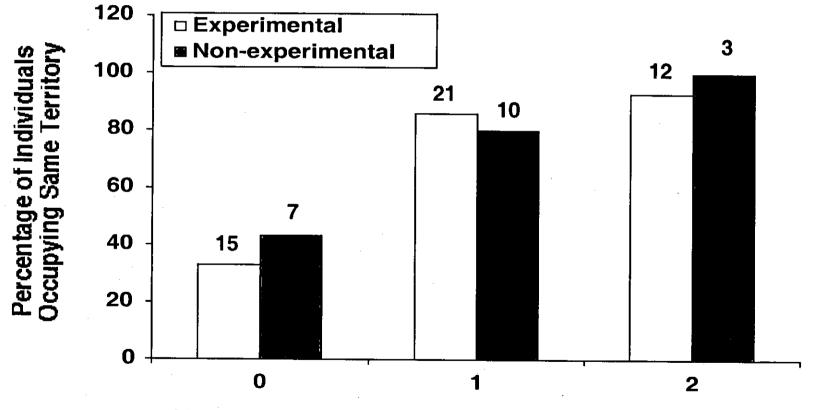


Number of Nesting Successes in Previous Year

Figure 19.

Between-Year Territory Fidelity of Males

(for individuals that returned to study sites in 1998)



Number of Nesting Successes in Previous Year

Figure 20.

Between-Year Returns of Unsuccessful Males

(for individuals nesting on study sites 1997-1998)

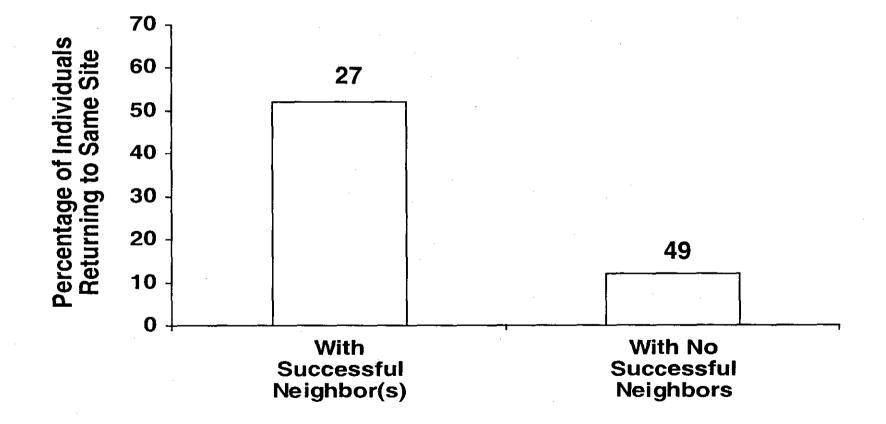


Figure 21.

