3) Do baseline stress hormones (i.e., corticosterone) vary in relation to conspecific density?

To our knowledge, no prior research has focused on physiological responses to density in wild songbirds. We predicted that if density had a negative impact on reproductive success, then we should also see elevated baseline corticosterone levels in our warblers with more neighbors. This prediction is based on prior research showing that chronic stress (i.e., prolonged elevated baseline corticosterone) can trigger behavioral and physiological effects that lead to decreased reproduction in vertebrates (McEwen and Wingfield 2003, Wingfield and Sapolsky 2003).

METHODS

Study Area & Study Organism

We conducted our research within the Cache River Watershed (CRW) in southern Illinois, USA. The CRW contains a diversity of habitat types within an agricultural matrix, and wet forest habitats, including bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) swamps, occupy ~9% of the landcover (Mankowski 1997).

The Prothonotary Warbler is a neotropical migrant that breeds in the eastern and central U.S. (Petit 1999). The species is a cavity-nesting habitat specialist that associates closely with water in bottomland forests and swamps. Prothonotary Warblers are territorial, socially monogamous, readily accept nest boxes, and exhibit high site fidelity between breeding seasons (Hoover 2003a), making them an ideal organism for experimental studies.

Density Manipulation & Determination of Breeding Densities

In 2008, we established a grid-system of 340 nest boxes on two 50 ha study sites in the CRW. At each site, we randomly established two 12.5 ha low-density and two 12.5 ha high-density subplots to control for potential habitat differences within each site. Low-density subplots had boxes spaced 80-100 m apart; high-density subplots had boxes spaced 35-50 m apart. During the 2008-2011 breeding seasons, we monitored and recorded the status of each box. We placed all boxes that had active warbler nests onto greased poles to eliminate nest predation. We also removed Brown-headed Cowbird (*Molothrus ater*) eggs during early incubation to eliminate confounding effects that occur when adult warblers raise cowbird young (Hoover 2003b). To facilitate identification of breeding pairs, all warblers using nest boxes and nearly all adult warblers seen at each site were captured and color-banded with a unique combination of a numbered aluminum leg band (U.S. Geological Survey) and colored plastic leg bands. We took standard mass, wing, and tarsus measurements for each adult and aged them as either second-year (i.e., 1 yr old and entering its first breeding season) or after-second year (i.e., ≥2 yrs old)(Kowalski 1986, Pyle et al. 1987) birds.

We mapped the location of every nest box using a Trimble GPS unit (Trimble Navigation Ltd., Sunnyvale, California) and transferred the coordinates into ArcGIS (ESRI, Redlands, California) to map the distance between nest boxes. We then calculated neighbor density as the number of warbler pairs within a 200-m radius of each active nest box. We felt this was the best measure of local density for a given breeding pair as previous work in the system has shown the warblers interact most with their neighbors within this distance (Schelsky 2010).

By removing nest predation and the effects of cowbird parasitism, we were able to increase the nesting success of the warblers, in turn increasing their site and territory fidelity between years. High site fidelity of returning birds combined with settlement of new birds led to increasing warbler densities each successive year. In 2008, densities ranged from 2-10 neighbors per warbler pair (EQ \O(x,¯) = 6 neighbors). Warbler densities peaked in 2010 with neighbor densities ranging from 1-27 neighbors (EQ \O(x,¯) = 14 neighbors). By 2011, warbler densities had stabilized with neighbor densities ranging from 2-23 neighbors (EQ \O(x,¯) = 14 neighbors).

Male Behavioral Observations

In 2010, when densities were at their maximum, we randomly chose banded males from both low- and high-density subplots for focal behavioral observations. When possible, we conducted observations throughout the nesting cycle (i.e., pre-incubation, laying, and nestling stages). We observed males during their first nesting cycle of the breeding season. Due to logistical and time constraints, not all males were observed across all stages, and some males were observed only once. Only one observer (S. Wheeler) conducted the behavioral observations. Observations were conducted between 0630-0930 hrs and prior to any other human activity at the male's nest box on that day. During a focal observation, a male was first located and observed for 30 s prior to the start of data collection. This helped reduce potential bias associated with conspicuous movements (e.g., flying; see Homes and Robinson 1988). Observed behaviors were continuously dictated into an mp3 voice recorder for later transcription. A stopwatch was used to keep time, and observation periods lasting less than 30 s were not transcribed. We followed a focal male until he was lost from sight for more than 30 s, until the observer became an apparent disturbance, or until the male had been observed for a total of 12 min in a day. All behaviors were categorized as either: song, walk, hop, flight, preen, sally strike, sally hover, glean, or probe. We did not differentiate between songs used for territorial defense (e.g., countersongs) and songs used for attracting females. Foraging movements and prey attack maneuvers were based on definitions provided by Holmes and Robinson 1988 (Table 1). We calculated counts and rates for each behavior for each male per observation period; rates are expressed as number per minute per nesting stage.

Warbler Reproductive Output

From late April through the beginning of August each year, we checked active nest boxes every 3-7 days. We also monitored natural cavity nests when they were found, but this was a rare occurrence (i.e., only 2 warbler pairs used natural cavities on our plots across the 4 yrs of our study). During each nest check, we recorded the host clutch size and cowbird egg status. We also identified adults that were present at the box or in the area. We determined nest initiation and hatch dates and always checked nests within 2