An integrative approach to testing density affects in a migratory songbird, the Prothonotary Warbler (Protonotaria citrea), in southern Illinois

## INTRODUCTION

Ecologists have long noted that many natural animal populations fluctuate around a long-term average abundance (Lack 1954). This abundance is thought to be regulated in part through density-dependent factors such as competition, predation, and disease. Once subject to debate (Murdoch 1994), ecologists now recognize density dependence as a conceptual cornerstone of population biology. Key questions persist, however, about the nature and generality of density effects. For example, even within a well-studied group such as songbirds, clear evidence for density dependence remains elusive (e.g., Brawn 1987, Both 1988, Torok and Toth 1988, Dhondt et al. 1992. Sillett et al. 2004). Although understanding the regulatory mechanisms controlling populations has proven difficult, it is considered to be one of the most important tasks still facing ecologists (May 1999). Indeed, many contemporary habitat issues (e.g., fragmentation, restoration) make it a priority to understand the basic processes underlying the dynamics of songbird populations if we are to effectively manage these populations and their habitats.

Although several density-dependent mechanisms may act to regulate a population, competition (e.g., for food, space) has often been assumed to be the most important mechanism regulating territorial songbirds in particular (Newton 1998). Most studies of density dependence in songbirds have focused on the associations between density and annual reproductive output that are expected when competition is intensified under crowded conditions (e.g., Alatalo and Lundberg 1984; Torok and Toth 1988; Both 1998). Very few studies have looked at how behavioral or physiological responses to density might mediate any potential negative density effects (Dobbs et al. 2007.



Prothonotary Warbler photo taken 31 May 2003 by Mary Kay Rubey.

Nephew and Romero 2003, Belden et al. 2007, Ortego and Espada 2007) despite the role that these responses have as proximate mechanisms underlying variation in fitness and survival (Wingfield and Sapolsky 2003). In reality, multiple mechanisms likely operate and interact to regulate populations (Krebs 2002, Rodenhouse et al. 2003), and understanding how behavior and physiology interact with density may be key to explaining the negative density effects, or lack thereof, detected in territorial songbird studies.

From 2008-2011, we used an experimental approach to test for multiple effects and mechanisms of density dependence on the breeding biology and physiology of a cavity-nesting songbird, the Prothonotary Warbler (*Protonotaria citrea*). We manipulated warbler density each season and collected data on male behavior, female reproductive output, and adult baseline stress hormones. Here, we report on the following general questions: Nicole Davros<sup>1</sup>, Stephanie Wheeler<sup>2</sup>, Wendy Schelsky<sup>3</sup>, Jeffrey Brawn<sup>4</sup>, and Jeffrey Hoover<sup>5</sup>

1) Does male behavior (i.e., song rates, foraging behavior) vary in relation to conspecific neighbor density?

We predicted that male competition for territories and mates, as measured by song rates, would increase in relation to conspecific neighbor density. We also predicted that increased neighbor density would lead to increased competition for food. Because measuring food directly can be quite difficult, we used prey attack rates, foraging movement rates, and flight rates as correlates for estimating food competition.

2) Does conspecific density influence measures of reproductive success?

We predicted that conspecific density would negatively influence reproductive success, leading to a decrease in correlates of reproductive success (e.g., clutch size, hatching success, fledging success, attempts at second broods) as well as total annual fledging production for females attempting second broods.

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- <sup>2</sup> School of Integrative Biology, U of I
- <sup>3</sup> Institute of Natural Resource Sustainability, Illinois Natural History Survey, U of I
- <sup>4</sup> Department of Natural Resources and Environmental Sciences, U of I
- 5 Institute of Natural Resource Sustainability, Illinois Natural History Survey, U of I\* \*University of Illinois

<sup>&</sup>lt;sup>1</sup> Program in Ecology, Evolution, and Conservation Biology, School of Integrative Biology, U of I