foraging movement rates during the peak of food demands (i.e., nestling stage) with increased neighbor density, but did not concomitantly increase their prey attack rates. Our results suggest that males had to work harder to find the same amount of food. However, we did not find any differences in fledging success or total annual fledgling production in relation to neighbor density. Thus, even if competition for food among males was greater with increased densities, it did not translate into any measurable effect on overall reproductive success. (Although we do not report on it in detail here, we also found no evidence that nestling provisioning rates nor nestling body condition prior to fledging varied in relation to density, which also lends support to our conclusion.) Further, our warblers did not show any differences in baseline plasma corticosterone levels in relation to density. Given that we did not detect any differences in reproductive output, the lack of differences in baseline stress levels is not surprising. Other studies have provided evidence for seasonal modulation of the stress response, indicating that migratory birds may express an "emergency life history stage" during which they respond to changing demands and environments in an adaptive manner to avoid the negative effects of stress (Wingfield et al. 1992, McEwen and Wingfield 2003). Additionally, there is growing evidence that individuals show consistent behavioral and physiological responses to dealing with stressors, and that these behaviors vary along a personality continuum ranging from shy to bold (Carere and Oers 2004, Bell et al. 2010). Bold individuals tend to be more aggressive and exploratory and capable of modulating their stress response; shy individuals tend to be the opposite. Although we attempted to control for potential differences in habitat that can lead to density-dependent reproduction, we could not control where our birds ultimately chose to settle within our sites. Therefore, it is possible that bold and shy birds sorted themselves into areas of conspecific density that they were physiologically capable of handling, thus using their own behaviors to mediate the effects of stress on reproductionSeveral other explanations for lack of density effects are possible as well. Density dependence via food competition may not be as important in this population of Prothonotary Warblers as it is for other songbird species. Bottomland hardwood forests provide some of the most productive habitat in North America and support a tremendous diversity of flora and fauna (Kellison and Young 1997, Kozlowski 2002), and competition for food may does not appear to be a limiting factor in southern Illinois swamps. We rarely observed starvation in our nests due simply to a lack of food during the 2008-2011 breeding seasons. Alternatively, male defense of their territories may have prevented the territories from becoming so small that food-limited reproduction could have occurred. Although we were unable to measure territory size directly ourselves, others have documented changes in territory size and subsequent foraging behaviors in relation to density (e.g., Sillett et al. 2004). The warblers may also have been trading current reproduction for future reproduction, thus overcoming potential negative effects of density reproductive output within a breeding season. As a species that faces unpredictable risks due to migration, Prothonotary Warblers may not sacrifice current reproductive output in response to density but rather self-maintenance (including survival). Our future work will test this hypothesis by comparing survival rates among adults with different neighbor densities. Finally, previous work in our study system has shown that nest predation on warbler nests is more closely tied to water depth, regardless of breeding bird densities (Hoover 2006), and is likely the major factor limiting warbler reproductive output. Extensive work has also shown that Brown-headed Cowbirds and blowfly (Protocalliphora spp.) ectoparasites play an important role in determining Prothonotary Warbler reproductive success in a given season (Hoover 2003b; N. Davros and W. Schelsky, personal observations). We believe our breeding population is more likely limited by these factors than traditional factors such as density-dependent food limitation.

Most ecologists would agree that multiple mechanisms likely interact to regulate populations (Krebs 2002, Rodenhouse et al. 2003), and there may not be one clear-cut answer to understanding how density influences reproductive output in different populations of songbirds. Future studies should continue to integrate long-term experimental manipulations along with tests of multiple potential density-dependent mechanisms in an attempt to better understand the role of each in regulating avian populations in different regions and habitats.

FUNDING

We are grateful for the support of the Illinois Ornithological Society and its members in helping to make this project possible. Additional funding support was provided by Champaign County Audubon Society (Charles Kendeigh Grant), American Ornithologists' Union (AOU Research Award), Sigma Xi (Grant-in-Aid of Research), North American Bluebird Society, American Museum of Natural History (Frank M. Chapman Award), Illinois Department of Natural Resources, The Nature Conservancy in Illinois, and the U.S. Fish and Wildlife Service. The Program in Ecology, Evolution, and Conservation Biology (PEEC), the School of Integrative Biology, and the Department of Natural Resources and Environmental Sciences (NRES) at the University of Illinois also provided funding.

ACKNOWLEDGMENTS

Jonathan Stein and Liz Pritchard provided assistance in data collection. Amber Albores and Matt McKim-Louder provided additional assistance and feedback on field methods. Tara Beveroth provided assistance with ArcGIS, and T.J. Benson, Emma Berdan, and Carla Caceres provided feedback on data analyses. Mike Brown, Liz Jones, and members of the Cache River Joint Venture Partnership (U.S. Fish and Wildlife Service – Cypress Creek National Wildlife Refuge, The Nature Conservancy, Illinois Department of Natural Resources, U.S. Department of Agriculture – Natural Resources Conservation Service, and Ducks Unlimited) provided logistical support for this project.