A MULTI-SCALE ANALYSIS OF COMPETITION BETWEEN THE HOUSE FINCH AND HOUSE SPARROW IN THE SOUTHEASTERN UNITED STATES

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Abstract. The decline of House Sparrow (*Passer domesticus*) populations in eastern North America has been proposed to be a consequence of competition between the House Sparrow and the House Finch (*Carpodacus mexicanus*), both introduced species. Previous research testing the hypothesis that House Sparrow declines are due to competition with House Finches focused on populations in the northeastern U.S., excluding other regions where the species coexist. We tested for effects of competition between these two species in the southeastern U.S. at two scales of analysis. First, we looked for evidence of competition at a local scale during the breeding season by examining patterns of co-occurrence of House Finches and House Sparrows at count points within a 28.3-km^2 study area centered on Auburn, Alabama. Second, we tested for the effects of competition at a regional scale across seven southeastern states by analyzing trends in Christmas Bird Count data. Using null-model analysis, we found no evidence for competitive exclusion in our assessment of local co-occurrence, suggesting that if there is competition between these species it is not important enough to affect their spatial distribution during the breeding season. At the regional scale, contrary to findings in the northeastern U.S., the decline of House Sparrow populations within the southeastern U.S. was not significantly correlated with House Finch abundance. Our results suggest that competition with House Finches is not a major cause of decline of the House Sparrow population in the southeastern U.S.

Key words: Carpodacus mexicanus, *co-occurrence, House Finch, House Sparrow, interspecific competition, invasive species,* Passer domesticus.

Análisis de Competencia en Múltiples Escalas entre *Carpodacus mexicanus* y *Passer domesticus* en el Sureste de Estados Unidos

Resumen. Se ha propuesto que la disminución de las poblaciones de *Passer domesticus* en el este de América del Norte es una consecuencia de la competencia entre *P. domesticus* y *Carpodacus mexicanus*, ambas especies introducidas. Investigaciones previas que evaluaron la hipótesis de que la disminución de *P. domesticus* es debida a la competencia con *C. mexicanus* se enfocaron en las poblaciones del noreste de EEUU, excluyendo otras regiones donde las especies coexisten. Evaluamos los efectos de la competencia entre estas dos especies en el sudeste de EEUU, considerando dos escalas de análisis. Primero, buscamos evidencia de competencia a escala local durante la estación reproductiva mediante el examen de patrones de co-ocurrencia de *C. mexicanus* y *P. domesticus* en puntos de conteo dentro de un área de estudio de 28.3 km^2 centrada en Auburn, Alabama. Segundo, evaluamos los efectos de la competencia a escala regional a través de siete estados del sudeste mediante el análisis de las tendencias en los datos del Conteo de Aves de Navidad. Usando análisis de modelos nulos, no encontramos evidencia de exclusión competitiva en nuestra evaluación de co-ocurrencia local, sugiriendo que si hay competencia entre estas especies no es de una importancia suficiente como para afectar su distribución espacial durante la estación reproductiva. A escala regional, contrariamente a los hallazgos en el noreste de EEUU, la disminución de las poblaciones de *P. domesticus* en el sudeste de EEUU no se correlacionó significativamente con la abundancia de *C. mexicanus*. Nuestros resultados sugieren que la competencia con *C. mexicanus* no es una causa importante de la disminución de las poblaciones de *P. domesticus* en el sudeste de EEUU.

INTRODUCTION

Competition plays a central role in many ecological processes including community structuring and species divergence (MacArthur 1972, Wiens 1989, Tilman 1994). However, the effects of competition are often not apparent at all scales of investigation (Diamond and Case 1986, Wiens et al. 1987, Bennett 1990), and the importance of competition can depend upon resource abundance and competitor density (Cody 1974, Cresswell 1997, 1998). Competition involving invasive species is a particularly relevant form of interspecific competition because introduced species are a major cause of declines of native species. While much of the literature concerning the effects of invasive species focuses on plants, insects, and pathogens, introduced birds can also have serious negative effects on native bird species (BirdLife International 2000). Birds are

ideal organisms for assessing the effects of introduced species because across most regions of the world census data are more complete for birds than for any other organisms. Therefore, the introductions of the House Sparrow (*Passer domesticus*) and, later, the House Finch (*Carpodacus mexicanus*) to eastern North America present opportunities for study of the interactions between an established species and a newly expanding species.

The House Sparrow was first successfully introduced to New York City in 1853 (Barrows 1889). Deliberate introductions in other cities along with rapid population growth and unaided dispersal led to the species' spread across the continent by 1900 (Barrows 1889, Robbins 1973, Bennett 1990). When the House Sparrow invaded the native range of the House Finch, a species with which it shares urban habitat, in western North America, interference competition between the two species was observed (Bertgold 1913, Kalinoski 1975). For instance, Bertgold (1913) reported House Sparrows destroyed 16% of House Finch eggs and young in Denver despite his efforts to protect the House Finch nests.

The House Finch was introduced from western North America into New York City in 1940 (Elliot and Arbib 1953) and subsequently spread across the eastern portion of North America (Veit and Lewis 1996, Gammon and Maurer 2002). Concurrent with the increase of the House Finch population in eastern North America was a decline in House Sparrow numbers in the same regions, prompting suggestions that competition with the House Finch caused the declines in House Sparrow populations (Kricher 1983, Wootton 1987, Cooper et al. 2007). Bennett (1990) summarized the value of the House Sparrow/House Finch system for studies of competition: (1) both introductions are recent, so sympatric evolution is unlikely to have reduced competition; (2) the species interact in an urban environment and so are somewhat isolated from other, confounding species; (3) both introductions and subsequent invasions are well documented.

Although the House Sparrow was in decline before the introduction of the House Finch (Hill 2002:23, Sauer et al. 2008), past empirical studies suggest that the House Finch invasion accelerated House Sparrow declines in eastern North America. Across the northeastern U.S., House Sparrow populations are negatively correlated with House Finch populations (Kricher 1983). Wootton (1987) found that House Sparrow declines accelerated after the House Finch invasion. Bennett (1990) found evidence for competition only at the continental scale. Cooper et al. (2007) found that House Sparrow populations rose after House Finch populations fell because of a disease outbreak and that House Finch abundance was highly correlated with the rate of House Sparrow decline.

These studies focused on the interaction of House Finches and House Sparrows in the northeastern U.S. Other portions of eastern North America, including the Southeast, have been excluded from study except for analysis of House Sparrow declines prior to the House Finch invasion (Kricher 1983, Bennett 1990). Both the House Sparrow and House Finch are less abundant in the southeastern U.S. than in the northeastern U.S. (Sauer et al. 2008), which may lessen the effects of competition on population dynamics and co-occurrence patterns.

Competition is not always apparent at all scales of investigation (Wiens 1989, Bennett 1990). Because competition theory predicts that interference competition between species should lead to temporal or spatial segregation of habitat (Cody 1974, Maurer 1984), competition may be more apparent at a local or habitat-level scale. Bennett (1990) found no evidence of segregation of House Sparrows and House Finches on the basis of the Christmas Bird Count (CBC)—in which birds are counted within a circle of 452 km^2—and he explained this lack of effect may arise because birds segregate at a local scale within urban, suburban, and rural habitats. Bennett (1990) suggested competition should be more apparent on the local scale because House Sparrows restrict House Finches to the areas between their colonies.

The goal of this study was to evaluate the effects of competition between the House Sparrow and House Finch in the southeastern U.S. at two distinct scales. First we tested for competitive exclusion between the two species at a local scale by examining their patterns of co-occurrence at point locations within a 28.3-km^2 study area centered on Auburn, Alabama. For this local (or sublocal, according to the terminology of Bennett 1990) analysis, we compared observed patterns of co-occurence to a null model, which is widely viewed as the most appropriate tool for revealing spatial patterns within a community (Gotelli 2001). If competition is important in determining the distribution of either or both species, we predicted that we would detect competitive exclusion between them. We also examined evidence for competition between the House Finch and House Sparrow on a regional scale by analyzing trends in Christmas Bird Count data from seven southeastern states. If competition between these two species is important throughout their shared range, we predicted that we would find a negative correlation between the House Sparrow's population growth rates and the House Finch's population size. Using the methods of Cooper et al. (2007), we examined CBC data from the southeastern United States for evidence for such an association.

METHODS

STUDY AREA AND BIRD SURVEYS

Local scale. Auburn, Alabama, has a human population size of approximately 55 000 (U.S. Census Bureau 2007) and is located in Lee County on the edge of the East Gulf Coastal Plain. We established a circular study area centered on the Auburn University campus and extending to a radius of 3 km (28.3 km^2), encompassing most of the city of Auburn. Within this study area we defined a grid of 443 points separated by 250 m.

Major habitat types in the study site include low-, medium-, and high-intensity urban development, pine forest, mixed pine/hardwood, and agricultural land. We surveyed each point for birds with a 5-min point count (Hutto et al. 1986) between 24 May and 24 June 2005, from 05:00 to 11:00 CDT.

Regional scale. We obtained CBC data for Alabama, Georgia, Florida, Mississippi, North Carolina, South Carolina, and Tennessee through the National Audubon Society's website, http://www.audubon.org/bird/cbc. Volunteers search each CBC circle for birds for 24 hr once annually between 14 December and 5 January.

STATISTICAL ANALYSES

Local scale. We organized count data into a presence–absence matrix in which rows represented the species and columns represented survey points. Entries in the matrix were either presence (1) or absence (0) of each species at each survey location (Simberloff and Connor 1979). We analyzed co-occurrence with EcoSim 7.0 (Gotelli and Entsminger 2006, Zhang et al. 2009), which calculates a measure of the number of survey points at which both species occurred (*c*-score, Stone and Roberts 1990) and then compares it to *c*-scores generated from 5000 random null distributions (Gotelli 2000). Briefly, the *c*-score is calculated as $(R_i - S)(R_j - S)$, where R_i is the number of occurrences of species *i*, R_j is the number of occurrences of species *j*, and *S* is the number of sites at which both occur. The greater the value of the *c*-score, the less frequently the two species are found together. We created null distributions by shuffling the data in a fashion that maintained the number of species occurrences but left each site with an equal probability of being occupied. The *c*-score has been shown to be robust, and our reshuffling method has been shown to minimize type I and II errors when sample data are used (Gotelli 2000, Sanders et al. 2003). We calculated *c*-scores for each null distribution and used them to create a histogram with which we calculated the probability of obtaining our observed *c*-score (Gotelli and Entsminger 2006). An observed *c*-score that is significantly greater than the mean *c*-score of the null distributions suggests competition (Gotelli 2000, Veech 2006). We calculated the standard effect size (SES) as (observed *c*-score − mean of simulated *c*-scores)/standard deviation of simulated *c*-score (Gurevitch et al. 1992, Zhang et al. 2009). An SES >2.0 suggests species segregation, whereas an SES of less than –2.0 suggests aggregation. Because habitat heterogeneity may bias results (Gotelli 2000), we analyzed co-occurrence in a subset of survey locations around which >50% of pixels in a 100-m circular buffer were classified as developed at medium or high intensity according to the Alabama Gap Analysis Program land-cover map (Kleiner et al. 2007). The choice of a 50% cutoff was arbitrary, but we believe that it is a reasonable threshold and that its use does not bias our inferences.

Regional scale. Our second approach to testing for negative effects of interspecific competition of the House Finch

and House Sparrow entailed the use of historical population trends of both species. As put forth by Cooper et al. (2007), a negative association between House Finch abundance and the growth rate of House Sparrow populations, revealed through the assessment of long-term population trends, would support the hypothesis that competition with the House Finch is a causal factor in the decline of the House Sparrow. We extended the analysis by Cooper et al. (2007) of House Finch abundance in relation to the House Sparrow's population growth rates to the southeastern U.S. to test whether evidence for competition in this region of the country is consistent with that in the Northeast.

We corrected abundance estimates from the survey data for each circle-year by using the standard approach of dividing the total number of individuals of each species observed during the survey by the total duration in hours of the survey. This correction yielded the number of birds per party-hour that we then used in developing statistical models. Additionally, before correcting for survey duration, we increased all raw abundance values of zero by 0.5 to avoid loss of data that would have resulted from taking the natural log of or dividing by zero in developing models described below.

Following the methods of Cooper et al. (2007), we developed a linear mixed model to investigate the effect of House Finch abundance in each CBC circle on the House Sparrow's population growth rate after controlling for the effect of intraspecific competition. In each model, the response variable—the growth rate of the House Sparrow population ($\ln \text{HOSP}_{t+1}/\text{HOSP}_t$)—was modeled as a function of the fixed effects and a random intercept. The fixed effects we considered for inclusion in model development were House Sparrow abundance (HOSP_t), House Finch abundance (HOFI_t), and the intercept to account for partial correlation of observations within the same CBC circles with error structure of variance components.

Differences between results of our regional-scale analysis for the Southeast and that of Cooper et al. (2007) for the Northeast could have resulted from different methodologies or from the lower statistical power of our analysis rather than from a true difference in trends between the two regions. To test for such an effect, we repeated our comparison after making the data sets more comparable. First, we followed the methods used by Cooper et al. (2007) in preparation of their dataset for analysis, not incrementing abundances by 0.5 and excluding all circle-years during which the House Sparrow was observed at a rate >30 birds party-hr^{-1} or the House Finch was observed at a rate >15 birds party-hr^{-1}. Cooper et al. (2007) also excluded observations of nonflocking species encountered at high rates, but they did not give specific details so we did not attempt to replicate this rule for observation exclusion. Second, to make the sample sizes in the two datasets equivalent, we randomly sampled numbers of sites and observations from the Northeast dataset equal to those in the

Southeast dataset. To do this, we used the "ranuni" command in SAS to sample sites without replacement, with the number of sites sampled equivalent to the number of sites in the Southeast dataset. We then exported all yearly records for these selected sites to a spreadsheet and assigned random numbers to each record in the dataset. Next we selected the record within each site with the lowest random number assigned to it for inclusion in the final sample, so that each site would be represented by at least one year. Finally, we assigned site-years in the final dataset on the basis of the order of the random number assigned to them until the number of total site-years in the dataset was equal to the number in the Southeast dataset. We then developed new models for the House Sparrow's population growth rate as in the first analysis by using both of these

datasets in separate models to determine whether the trends were consistent with those from our first analysis and those published by Cooper et al. (2007).

We specified all models for the regional analyses with PROC MIXED in SAS version 9.1.

RESULTS

LOCAL SCALE

We detected 244 House Finches at 78 sites and 258 House Sparrows at 64 sites (Fig. 1). We focused on areas developed at medium and high intensity, in which House Finches were detected at 23 sites, House Sparrows at 26 sites, and at least one of either species at 38 sites. Within these areas, we found the species
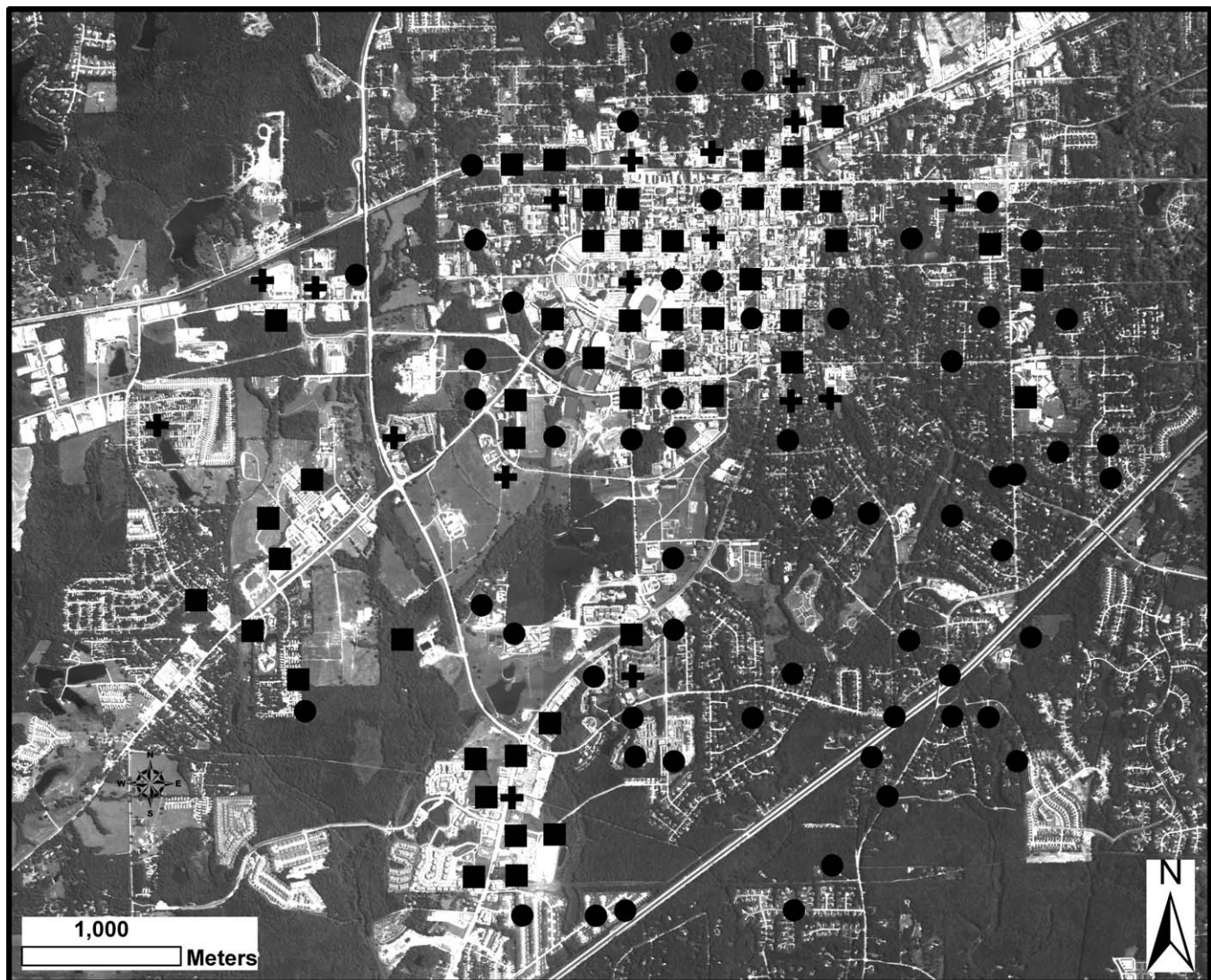

FIGURE 1.   Aerial photo of Auburn, Alabama, showing locations where House Finches (circles), House Sparrows (squares), or both (plus signs) were detected.

together at 11 sites, yielding a *c*-score that was not significantly different from the randomly generated *c*-scores (observed *c*-score = 180, mean null *c*-score = 222, $P = 0.35$, SES = –0.74).

REGIONAL SCALE

The CBC database contained 205 CBC circles throughout the Southeast for the period 1970–2008, and the number of years per circle ranged from 1 to 38. Across the region, the mean abundance of the House Sparrow was 1.42 birds party-hr^{-1} (SD = 2.44) and that of the House Finch was 1.35 birds party-hr^{-1} (SD = 1.96).

The coefficient for the fixed effect of initial House Sparrow abundance in the model for the first regional analysis of the House Sparrow's population growth rates was significantly less than zero, with $\alpha = 0.05$ ($\beta_1 = -0.048$, SE = 0.004, $t_{2300} = -12.52$, $P < 0.001$; Fig. 2a), indicating a negative association between the mean growth rates of House Sparrow

populations and the degree of intraspecific competition they experienced. However, the coefficient for the fixed effect of House Finch abundance was not significantly different from zero ($\beta_2 = -0.005$, SE = 0.005, $t_{2300} = -1.09$, $P = 0.277$; Fig. 2b), suggesting a lack of influence of House Finch abundance on the House Sparrow's population growth rates in the CBC circles throughout the Southeast.

Our second regional analyses were designed to be comparable to the analyses of Cooper et al. (2007). For the model of the House Sparrow's population growth rate in the Southeast in this second analysis, the coefficient for House Sparrow abundance was negative ($\beta_1 = -0.098$, SE = 0.009, $t_{2283} = -10.54$, $P < 0.001$), and the coefficient for House Finch abundance was not significantly different from zero ($\beta_2 = -0.019$, SE = 0.012, $t_{2283} = -1.52$, $P = 0.128$). In the model for the Northeast, coefficients of House Sparrow and House Finch abundance were both negative (House Sparrow: $\beta_1 = -0.045$, SE = 0.003, $t_{2283} = -16.24$, $P < 0.001$; House Finch: $\beta_2 = -0.010$, SE = 0.004, $t_{2283} = -2.66$, $P = 0.008$). Thus trends in the second regional analyses mirrored those of our first regional analysis and those presented by Cooper et al. (2007), suggesting that differences in inference were not due to differences in how the datasets from either region were analyzed or to differences in sample size, and thus statistical power, between the two datasets.

DISCUSSION

In the latter part of the 20th century, numbers of House Finches in the eastern U.S. and southern Canada increased dramatically. Over a similar period, populations of House Sparrows declined steadily and persistently throughout the eastern U.S. (Kricher 1983, Wootton 1987, Bennett 1990, Summers-Smith 2003, Cooper et al. 2007). These authors hypothesized that the decline of the House Sparrow, at least in the eastern portion of the continent, was causally linked to increasing numbers of the House Finch. Anecdotal observations of the two species interacting competitively supported the idea that these interactions could affect the species' abundances, but rigorous testing of the hypothesis required more careful and detailed analyses.

Studies of bird-census data in the northeastern U.S. suggested that the invasion of the House Finch accelerated the decline of the House Sparrow in that region (Kricher 1983, Wootton 1987, Bennett 1990, Cooper et al. 2007). In our study, however, we found no evidence for competition between the House Sparrow and House Finch in the southeastern U.S. at either a regional or local scale. In our analysis of regional trends, we found no significant association between House Finch abundance and rate of decline of the House Sparrow. This result is in contrast to the negative association between the two species reported by Cooper et al. (2007) in the Northeast, confirmed by our reanalysis of their data. Therefore, if competition exists at a regional scale in the southeastern U.S. as
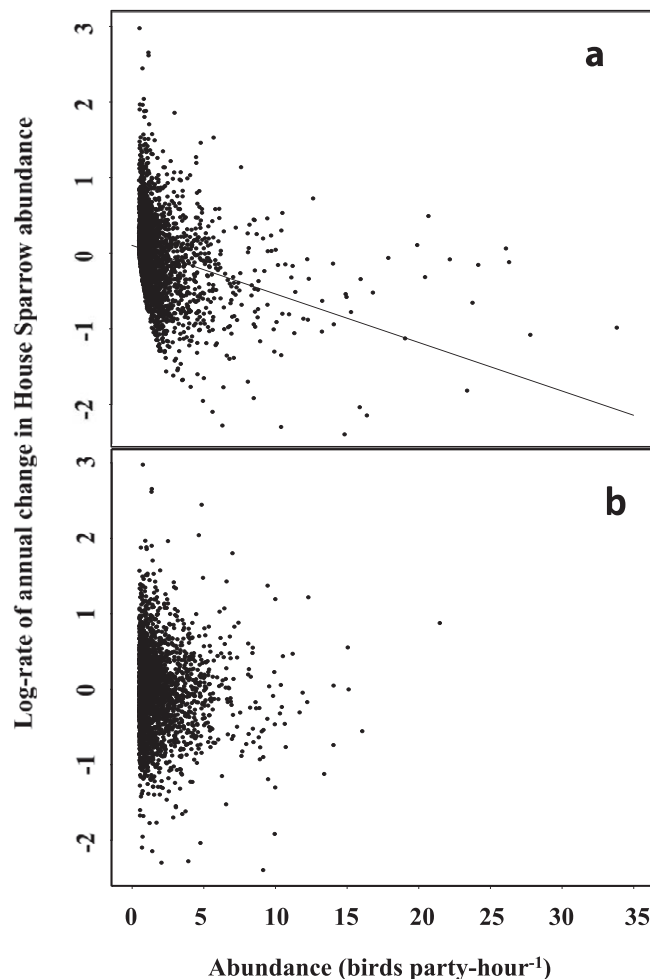
FIGURE 2.   Log-transformed growth rate of the House Sparrow population versus House Sparrow abundance (a) and House Finch abundance (b). Dots represent individual Christmas Bird Count circles within the southeastern U.S.

appears to be the case in the northeastern U.S., it is too weak to be statistically demonstrated with CBC data. After an epizootic of *Mycoplasma gallicepticum*, Cooper et al. (2007) also found a decline in northeastern House Finch populations that coincided with a rise in House Sparrow populations, providing evidence for competition in that region. We were unable to test for this second relationship because the House Finch's invasion of many parts of the Southeast coincided with onset of the epizootic (Hill 2002).

We also tested for effects of competition at a local scale by examining patterns of co-occurrence between House Sparrows and House Finches within 28.3 km^2 in central Alabama, finding no evidence that these two species exclude one another at this local scale. Around Auburn, there was no pattern consistent with competitive exclusion during the breeding season. Bennett (1990) suggested that while he found no evidence for competition in data from CBC circles pooled, there may be competition at a local scale within a circle. Our results suggest that in the southeastern U.S. interference competition between these species is insufficient to force them to segregate at any scale.

Accounts of the outcome of interspecific encounters between House Sparrows and House Finches suggest that interactions between these species may be different in the western part of the continent than in the East. In the West, House Sparrows have been reported to dominate House Finches both in the wild and in aviary experiments (Bent 1968, Kalinoski 1975). Bennett (1990) suggested that while the House Sparrow may win in aggressive encounters it still incurs an energetic cost that may manifest itself in population declines. Dispersive birds, however, tend to be more aggressive than their sedentary counterparts (Duckworth 2008). Wootton (1987) and Cooper et al. (2007) suggested that the invasive eastern House Finches are more aggressive than finches in western populations from which they originated and that aggressive eastern House Finches may have a greater effect on the House Sparrow's population dynamics. If the House Finch is dominant over the House Sparrows in the East, we should see evidence of competition on a local scale. Our results, however, show that neither species is being excluded from the House Sparrow's preferred urban habitat.

Cooper et al. (2007) reported evidence of competition between the House Sparrow and House Finch on the basis of the CBC, but they were unable to detect the same trend with Breeding Bird Survey (Sauer et al. 2008) data. The failure to find such a trend with the Breeding Bird Survey may be due to differences in sample size or sampling schemes (Cooper et al. 2007). Cooper et al. (2007) suggested that, at a minimum, their results reveal competition in the winter and that changes in winter abundance should correlate with changes in summer abundance. We were unable to detect evidence of competition at a local scale during the breeding season or at a regional scale during the winter. Therefore, we found no evidence of competition at any time of year in the southeastern U.S.

The lack of evidence for competition between these species in the Southeast, despite the predictions of competition theory (Cody 1974, Maurer 1984, Bennett 1990) and anecdotal evidence of exclusion in the Northeast (Kricher 1983), may be due to the densities of the two competitors. Effects of competition are greater and easier to detect when competitors' densities are higher (Schoener 1983, Cresswell 1997). Both the House Sparrow and House Finch are substantially more abundant in the northeastern than in the southeastern U.S. (Sauer et al. 2008). Therefore, densities in the Southeast may not be high enough to affect the species' distributions through competition or yield a statistically detectable effect. Nonetheless, within the seven-state region we analyzed, the House Sparrow showed the same pattern of decline as in the Northeast. The fact that competition does not seem to be responsible for the decline of the House Sparrow in the Southeast suggests that a factor other than competition is the primary cause of the House Sparrow's declines across North America.

ACKNOWLEDGMENTS

LITERATURE CITED

BARROWS, W. B. 1889. The English Sparrow (*Passer domesticus*) in North America, especially in its relations to agriculture. Bulletin 1. U.S. Department of Agriculture, Division of Economic Ornithology and Mammalogy, Washington, D.C.

BENNETT, W. A. 1990. Scale of investigation and the detection of competition: an example from the House Sparrow and House Finch introductions in North America. American Naturalist 135:725–747.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies, part 1. Dover Press, New York, NY.

BERTGOLD, W. H. 1913. A study of the House Finch. Auk 30:40–73.

BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Birdlife International, Cambridge, UK.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, NJ.

COOPER, C. B., W. M. HOCHACHKA, AND A. A. DHONDT. 2007. Contrasting natural experiments confirm competition between House Finches and House Sparrows. Ecology 88:864–870.

CRESSWELL, W. 1997. Interference competition at low competitor densities in Blackbirds *Turdus merula*. Journal of Animal Ecology 66:461–471.

CRESSWELL, W. 1998. Relative competitive ability changes with competitor density: evidence from feeding blackbirds. Animal Behaviour 56:1367–1373.

DIAMOND, J., AND T. J. CASE. 1986. Community ecology. Harper and Row, New York.

DUCKWORTH, R. 2008. Adaptive dispersal strategies and the dynamics of a range expansion. American Naturalist 172:S4–17.

ELLIOT, J. J., AND R. S. ARBIB. 1953. Origin and status of the House Finch in the eastern United States. Auk 70:31–37.

GAMMON, D. E., AND B. A. MAURER. 2002. Evidence for non-uniform dispersal in the biological invasions of two naturalized North American bird species. Global Ecology and Biogeography 11:155–162.

GOTELLI, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621.

GOTELLI, N. J. 2001. Research frontiers in null model analysis. Global Ecology and Biogeography 10:337–343.

GOTELLI, N. J., AND G. L. ENTSMINGER. 2006. EcoSim: null models software for ecology, version 7.0. Acquired Intelligence, Inc., and Kesey-Bear, Jericho, VT.

GUREVITCH, J., L. L. MORROW, A. WALLACE, AND J. S. WALSH. 1992. A meta-analysis of competition in field experiments. American Naturalist 140:539–572.

HILL, G. E. 2002. A red bird in a brown bag. Oxford University Press, New York.

HUTTO, R. L., S. M. PLETSCHET, AND P. HENDRICKS. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593–602.

KALINOSKI, R. 1975. Intra- and interspecific aggression in House Finches and House Sparrows. Condor 77:375–384.

KLEINER, K. J., M. D. MACKENZIE, A. L. SILVANO, J. A. GRAND, J. B. GRAND, J. HOGLAND, E. R. IRWIN, M. S. MITCHELL, B. D. TAYLOR, T. EARNHARDT, E. KRAMER, J. LEE, A. J. MCKERROW, M. J. RUBINO, K. SAMPLES, A. TERANDO, AND S. G. WILLIAMS [ONLINE]. 2007. GAP land cover map of ecological systems for the state of Alabama (provisional). <http://www.auburn.edu/academic/forestry_wildlife/alabama_gap_analysis_project/AL-GAP%20land%20cover%20map%20metadata.htm> (28 January 2008).

KRICHER, J. C. 1983. Correlation between House Finch increase and House Sparrow decline. American Birds 37:358–360.

MACARTHUR, R. H. 1972. Geographical ecology. Patterns in the distribution of species. Harper and Row, New York.

MAURER, B. A. 1984. Interference and exploitation in bird communities. Wilson Bulletin 96:380–395.

ROBBINS, C. S. 1973. Introduction, spread, and present abundance of the House Sparrow in North America. Ornithological Monographs 14:3–9.

SANDERS, N. J., N. J. GOTELLI, N. E. HELLER, AND D. M. GORDON. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences of the United States of America 100:2474–2477.

SAUER, J. R., J. E. HINES, AND J. FALLON [ONLINE]. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007, version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html> (6 December 2009).

SCHOENER, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

SIMBERLOFF, D., AND E. F. CONNOR. 1979. Q-mode and R-mode analyses of biogeographic distributions: null hypotheses based on random colonization, p. 123–138. In G. P. Patil and M. L. Rosenzweig [EDS.], Contemporary quantitative ecology and related ecometrics. International Cooperative Publishing House, Fairland, MD.

STONE, L., AND A. ROBERTS. 1990. The checkerboard score and species distributions. Oecologia 85:74–79.

SUMMERS-SMITH, J. D. 2003. The decline of the House Sparrow: a review. British Birds 96:439–446.

TILMAN, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

U.S. CENSUS BUREAU. 2007. Annual estimates of the population for incorporated places in Alabama, April 1, 2000 to July 1, 2006. SUB-EST2006-04-01. Census Bureau, Washington, DC.

VEECH, J. A. 2006. A probability-based analysis of temporal and spatial co-occurence in grassland birds. Journal of Biogeography 33:2145–2153.

VEIT, R. R., AND M. A. LEWIS. 1996. Dispersal, population growth, and the Allee effect: dynamics of the House Finch invasion of eastern North America. American Naturalist 148:255–274.

WIENS, J. A. 1989. The ecology of bird communities, vol. 2. Processes and variations. Cambridge University Press, Cambridge, UK.

WIENS, J. A., J. T. ROTENBERRY, AND B. V. HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147.

WOOTTON, J. T. 1987. Interspecific competition between introduced House Finch populations and two associated passerine species. Oecologia 71:325–331.

ZHANG, J., Z. HAO, B. SONG, B. LI, X. WANG, AND J. YE. 2009. Fine-scale species co-occurrence patterns in an old-growth temperate forest. Forest Ecology and Management 257:2115–2120.