House Finch (Carpodacus mexicanus) Population-and Group-Level Responses to a Bacterial Disease

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CHAPTER 2

HOUSE FINCH (*CARPODACUS MEXICANUS*) POPULATION- AND GROUP-LEVEL RESPONSES TO A BACTERIAL DISEASE

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ABSTRACT.—We examined changes in group sizes of House Finches (*Carpodacus mexicanus*; hereafter "finches"), at feeders over the course of establishment of a novel disease caused by the bacterium *Mycoplasma gallisepticum*. Our goal was to identify factors linked with the severity of decline in sizes of finch groups, with the aim of inferring causes of variation in rates of disease transmission and disease-induced mortality. We found that only site-specific density-dependence consistently predicted the sizes of declines in finch group sizes. By contrast, there were no differences in declines among habitats known to differ in finch abundance, or among regions with different overall abundances of finches. We also failed to find differences in declines along a gradient of winter temperature. Our results suggest that the effects of disease on host populations in this system are primarily determined by interactions among finches at individual sites, with little consistent influence of factors extrinsic to these local groups.
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RESUMEN.—Examinamos los cambios en el tamaño de grupos de *Carpodacus mexicanus* en los alimentaderos durante el establecimiento de una enfermedad nueva causada por la bacteria *Mycoplasma gallisepticum*. Nuestra meta fue el identificar los factores asociados con la severa reducción en el tamaño de los grupos de *C. mexicanus*, con el objetivo de inferir causas en la tasa de transmisión de la enfermedad y de mortalidad debido a la enfermedad. Encontramos que solamente factores denso-dependientes y específicos a un sitio, predijeron constantemente las dimensiones de las reducciones en el tamaño de los grupos de *C. mexicanus*. En contraste, no hubo diferencias en las reducciones entre los habitats que se sabia que se diferenciaban en cuanto a abundancia de *C. mexicanus*, o entre regiones con diferentes abundancias de *C. mexicanus*. No pudimos encontrar diferencias en las reducciones a lo largo de un gradiente de temperaturas invernales. Nuestros resultados sugieren que los efectos de la enfermedad en la población hospedera en este sistema están principalmente determinados por interacciones entre *C. mexicanus* en sitios únicos, con poca influencia de factores extrínsecos a esos grupos locales.

WHEN A NEW parasite or predator is introduced into a host population, the resulting population fluctuations can range from unstable oscillations that may lead to extinction of one of the pair to a monotonic equilibrium without oscillations. In host–disease systems, the rate of transmission of disease between hosts and the severity of the disease's effects are two of the key parameters that determine the pattern of change in host abundance. Thus, a clear understanding of host–disease dynamics can only be obtained following identification of the factors that affect rates of disease transmission and the subsequent probability of mortality. However, direct identification of these factors can be extremely difficult, especially for disease transmission rates in wild populations of animals. For a social species, one indirect method of inferring variation may be available, because transmission rate is likely to be affected by the sizes of groups in which animals interact (e.g. May and Anderson 1984). The disease will, in turn, affect the sizes of groups in which animals occur. Thus, any factor, such as group size or climatic severity, that is correlated with the size of a disease-induced population decline can be inferred to potentially mediate the rate of disease transmission or mortality following infection. Such inferences can be used

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to guide further research. That observation motivated the present study on House Finches (*Carpodacus mexicanus*; hereafter "finches") and their response to a bacterial disease organism, *Mycoplasma gallisepticum*.

Finches are peridomestic, monogamously breeding (Hill 1993), and, in eastern North America, semimigratory (Able and Belthoff 1998); outside of the breeding season, they spend their days in loose social groups of generally <50 birds, and their nights roosting solitarily or in groups of fewer than 10 birds (in the northeastern United States; Dhondt et al. 2006). A novel strain of *M. gallisepticum* first emerged as a disease organism of finches in the winter of 1993–1994 (Ley et al. 1996), with the bacteria transmitted either by direct contact or indirectly through fomites present on surfaces that come in contact with susceptible finches (Dhondt et al. 2005). Since emergence, the disease has spread rapidly (Dhondt et al. 1998), causing declines or halting finch population increases throughout eastern North America (Hochachka and Dhondt 2000). Disease prevalence varies seasonally (Altizer et al. 2004), with very few diseased birds observed during the breeding season. Since the initial declines, populations of finches have remained at low levels, with the *M. gallisepticum* persisting in all parts of the finch's eastern range. Such a pattern of monotonic decline followed by stability in host populations after emergence of a disease has almost never been noted (for an exception, see Sinclair [1977:222]). We are able to monitor this *Mycoplasma* bacterium in finches because it causes swollen conjunctiva that are visible from a distance (House Finch Disease Survey; see Acknowledgments), which allows us to solicit observations of diseased birds from the general public over much of North America. To date, all analyses describing the effects of mycoplasmal conjunctivitis in finch populations have described average changes in regional abundance of finches. The relationship between these regional changes and changes in local group sizes have not been explored in detail.

Prior work, both published and unpublished, has led us to four factors that might influence how disease affects the sizes of social groupings of finches, either through variation in rates of disease transmission or in severity of the effects of *M. gallisepticum* on finch populations. (1) Timing of annual disease outbreaks and prevalence of disease vary along a gradient of winter temperature (Altizer et al. 2004), so climatic severity may play a role. (2) A correlate of winter temperature is overall abundance of finches, with smaller groups of finches in warmer regions (Altizer et al. 2004). (3) Across this cold–warm gradient, birds are not distributed uniformly, and prior work (W. M. Hochachka unpubl. data) indicates that finch abundance varies systematically along local gradients of urbanization, with lowest abundance in the most highly urbanized environments. Thus, in the presence of density-dependent transmission (Hochachka and Dhondt 2000) and restricted finch movement (Dhondt et al. 2006), we would expect systematic variation in rates of finch decline across a gradient of urbanization. (4) More generally, any site-specific differences in finch group sizes may affect rates of disease transmission as well as social stress and resultant disease susceptibility (Hawley et al. 2006).

Our goal here is to identify which, if any, of these four factors affect rates of transmission of *M. gallisepticum* among finches, or rates of finch mortality following infection. We do this by testing whether any of these factors is related to the magnitude of declines in group size of finches in eastern North America, following the arrival and establishment of *M. gallisepticum* as a disease organism. Our objective is not to prove links between these factors and disease transmission or host mortality rates, but to identify a limited set of likely influences that can be examined subsequently in more detail. We first describe the patterns of geographic variation in social group sizes before and after establishment of *M. gallisepticum*. Using a subset of our data (all observers for which paired comparisons can be made across the 10-year period), we tested for effects of the four factors on sizes of decline in finch group sizes. Of the four—severity of winter cold temperatures, regional abundance of finches, extent of urbanization around a site, and site-specific abundances of finches before arrival of *M. gallisepticum*—only local predisease group sizes were related to rates of finch decline. We concluded our analyses by examining the degree of spatial autocorrelation in finch abundance, to explore the possibility that outbreaks of disease would be locally clustered in association with local clusters of sites with high finch densities.

Methods

Data Collection

To answer the questions outlined above, we analyzed data on local abundances of finches from a wide geographic area. These data were available to us because of a "citizen science" project, in which volunteer participants gathered data from a large part of the United States and Canada.

Data on sizes of social groups of finches are from Project FeederWatch (Wells et al. 1998, Lepage and Francis 2002), which is jointly managed by the Cornell Laboratory of Ornithology and Bird Studies Canada. Participants count the maximum number of birds seen simultaneously over the course of an observation period, which can vary from one to two days (typically all or part of a weekend). Observation periods are typically spaced at one- or two-week intervals, with a minimum of five days between consecutive observation periods. Observations are made from mid-November to the very beginning of April each year, with ≤20 observation periods by each participant. This overwinter interval corresponds roughly to the time of greatest mycoplasmal conjunctivitis prevalence in the northeastern United States and adjacent Canada (Altizer et al. 2004). Sizes of social groupings at feeders are a logical measure of finch abundance to examine in the context of host–disease dynamics (see below).

In addition to recording counts of birds and dates of observation, participants recorded supplementary information, including location, observer effort, and a description of habitat. Location information varied in precision. During the initial years, all locations were exclusively represented by U.S. five-digit zip codes or Canadian postal codes. In later years (starting in the 2000–2001 winter), participants who submitted their observations over the Internet were able to enter more exact locations determined using a variety of methods, including readings from global positioning system (GPS) units, readings from topographical maps, and an Internet-based map location tool. Roughly 45% of all locations, and 75% of all locations with data submitted over the Internet, were entered using these higher-precision methods. Observer effort (ordinal variable) is reported as the number of half-days during which observations were made in an observation period; higher effort leads to higher counts of birds. The habitat descriptor used in our analyses is the degree of urbanization, reported as one of four categories ranging from "rural" to "urban," which past experience has shown is a consistently important predictor of bird abundances. Although other habitat descriptors have predictive power, they are often not provided by project participants.

A problem in FeederWatch is that some participants fail to count the maximum number of birds seen at one time, instead summing all observations and thus recording individual birds multiple times. We estimate that this error occurs in ~3% of all data. Such cases were identified and removed by scanning all records for a number of widespread species that occur only in relatively small aggregations (Downy Woodpeckers [*Picoides pubescens*]; nuthatches, genus *Sitta*; chickadees and titmice, family Paridae) and eliminating all data from participants reporting excessively large numbers of at least one of these taxa.

We analyzed FeederWatch data from almost all states that lie east of the Mississippi River (Fig. 1). Data from Wisconsin, Michigan, Minnesota, and Florida were excluded, because of generally low abundances of finches across most of the areas of these states. Louisiana was the only state partially west of the Mississippi that we included; it was added to increase the sample of finches in the warmest winter areas. FeederWatch data from parts of Canada adjacent to our study region could not be used, because no geographic information system (GIS) layer of winter temperature data was available for Canada.

In addition to the data collected directly through FeederWatch, we used two other sources of data. The first was information on winter temperatures, used to characterize typical winter climate. The Spatial Climate Analysis Service (see Acknowledgments) provided fine-resolution interpolations of monthly mean winter temperatures in the period from 1971 to 2000 (inclusive). We used the lowest monthly mean from December, January, and February as our descriptor of winter temperature. The raster temperature data layers were associated with individual FeederWatch sites using ARCGIS, version 9.0. The other ancillary data, region-wide abundances of finches from the North American Christmas Bird Count (CBC), were used to increase the accuracy with which variation in observer effort was related to changes in detection probability (see below). Raw counts were converted to birds-per-party-hour for each site. We acknowledge that bird-per-party-hour is only a rough index of bird abundance (see Link and Sauer 1999), and use of this measure for comparisons among CBC locations assumes that the same or very similar biases will be manifested at all sites. Our past experience suggests that differences in abundance of birds across space are qualitatively similar, whether effort corrections are made using birds-per-party-hours or by more sophisticated means. Kriging, using PROC KRIGE2D in SAS, version 9.2, was used to interpolate site-specific abundances of finches for each FeederWatch site, with separate interpolations done for each winter season, using that winter's CBC data. The model used for kriging was for an exponential variogram, with nugget = 5, range = 12, and sill = 17; all "distance" units were in decimal degrees. We recognize that decimal degrees provide only approximate indices of distance, with a single degree latitude representing different distances than a degree longitude, and the

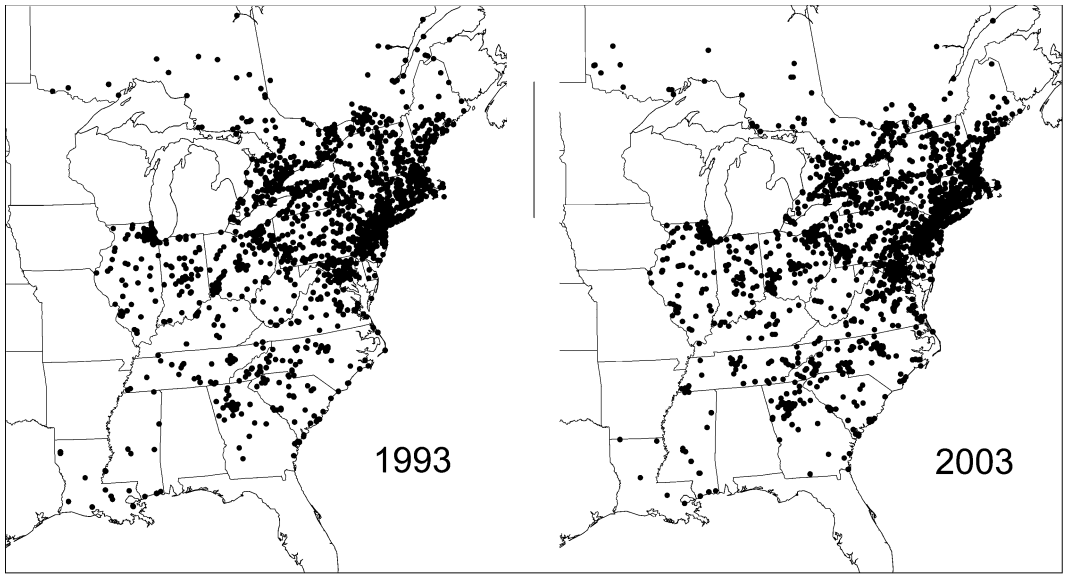

FIG. 1. Distribution of sites reporting House Finches from Project FeederWatch in the winters of 1992–1993 and 2002–2003. Although numbers of locations increased between these winters, overall distribution of data remained relatively constant. Locations of data that were analyzed are plotted.

relationship between distance and longitude varying from north to south. However, any method of obtaining distances from map projections would have some inherent inaccuracies over the areas considered here, and we believe that the broad-scale variation in abundance of finches across the eastern United States was captured in our approximation.

Statistical Analyses

Statistical models describing finch group size.— FeederWatch sites were not randomly located (Fig. 1) and were in a variety of environments, which creates challenges for translating the observed finch group sizes into a standardized index of group sizes and correctly identifying predictors of variation in group sizes. In particular, exploratory analyses of our data revealed that average observer effort varied across the eastern United States. Thus, geographic variation in observer effort could be confounded with geographic variation in abundances of finches, creating biases in the estimated relationship between observer effort and detection probability. We dealt with this issue by assuming that the relationship between observer effort and reported group size will change with the regional abundance of finches: in regions where finches are more abundant, less effort would be required to see the same-sized group of finches. A region-wide abundance * observer-effort statistical interaction proved consistently to be an important predictor, given that for all separate winters' data, the regression coefficients from this interaction differed from zero. Exploratory analyses suggested that the degree of variation in finch group sizes along a rural-to-urban gradient was also affected by overall abundance of finches within the region. We therefore included a region-wide abundance * urbanization statistical interaction in all our statistical models. For most but not all years of available data, we found that the regression coefficients from this interaction were statistically different from zero. Given the presence of a strong finch abundance * urbanization interaction in most years, we assumed it to be biologically real and retained the interaction in analyses of data from all years.

We also expected that the probability of a finch coming to a feeder would vary with the severity of winter cold stress. Knowing from previous experience that there are typically midwinter peaks in numbers of birds reported at feeders, we expected that these peaks would be greater in regions with colder minimum temperatures. Thus, we included a month * minimum-temperature interaction in our analyses. Regression coefficients from this interaction invariably differed from zero for all years of data analyzed.

In summary, the statistical model we used to describe variation in finch group sizes contained the following fixed-effect predictors: minimum mean monthly temperature of the coldest calendar month, calendar month, a minimum temperature * month interaction, regional (CBC) finch abundance, an urbanization * regional finch abundance interaction,

and an observer effort * regional finch abundance interaction. Only calendar month and urbanization were treated as categorical variables in our analyses. Because multiple data points were submitted from each location in a given winter, the non-independence of these data was taken into account using site as a random effect (SAS variance components type) in our analyses. FeederWatch data were fitted to this model, separately for each winter's data, producing effort-standardized indices of group sizes (e.g. Fig. 2). Model-fitting used PROC MIXED and the associated GLIMMIX macro in SAS 9.2. The GLIMMIX macro was used because group sizes are count data and the errors non-normally distributed; the macro allowed use of mixed-model Poisson regression analyses.

When data from a subset of observers were used in paired comparisons between years, similar statistical models were used. Only data from between December 16 and January 15 were used to examine the roughly decadal changes during the time of winter with maximum group sizes of finches at feeders. This period was chosen because preliminary analyses (W. M. Hochachka unpubl. data) showed that in all years, peak group sizes of finches were reported in the period between December and January. Because we used data from a restricted period, the month variable and its interaction were not included in the statistical models. Year (pre- and post-disease emergence) was added as a predictor variable to formally test for effects of various factors on the magnitude of declines in finch abundance. We examined the evidence that various factors affected magnitudes of declines by adding interaction terms to this base model. For example, to examine whether severity of winter cold affected the magnitude of the decline, we added a winter temperature * year interaction to the base model. Observations across years from the same site were treated as repeated measures, and we allowed for a different covariance structure for multiple observations at a site for each year in our random effects.

The four predictors examined using these interaction terms were regional predisease abundance of finches, site-specific predisease group sizes of finches, urbanization at the site, and minimum monthly winter temperature at the site. Of these, only the derivation of the site-specific abundances has not been described above. These values were finch group sizes from each site predicted for the actual observation date closest to 1 January 1993 from the same statistical model used to produce the 1992–1993 estimates in Figure 2. These predictors are undoubtedly highly correlated with the observed group sizes from the 1992–1993 data used as response variables in the repeated-measures analyses. However, we have no *a priori* reason to suspect that the predicted values will be related to the magnitude of changes in group size following arrival of disease for reasons that do not reflect true biological patterns. We used a multimodel inference approach (Burnham and Anderson 2002) to assess the relative importance of each of these factors for predicting changes in group sizes in our set of five models. The set (Table 1) contained a base model and one model containing a year * predictor interaction for each of the four hypothesized influences on the magnitudes of decline in group size.

In our paired comparisons, we used data from two winters only, 1992–1993 and 2002–2003. We did this, in part, to simplify interpretation of results, with a clear "before" and "after" allowing for several years of disease establishment and any possible transient dynamics to disappear. A further reason for this restriction was logistic: including multiple years' data overtaxed the available computers.

We compared the results from PROC MIXED and the GLIMMIX macro to those obtained from the currently experimental PROC GLIMMIX and from PROC MIXED when square-root-transformed counts of birds were used as the response variable. Results and conclusions were qualitatively the same, regardless of which approach was used, and only the results from the GLIMMIX macro analyses are presented.

Spatial autocorrelation in finch group sizes.—We examined the degree to which nearby sites were interconnected by movement of birds among sites by calculating spline correlograms (Bjørnstad and Falck 2001) using the ncl library in the R statistical package (R Development Core Team 2005). Spline correlograms provide nonparametric description of how correlations in measurements vary with the distance between pairs of sites, making no prior assumptions about the shape of this correlation–distance relationship. We reasoned that after our mixed-model statistical analyses have explained all the variation possible with a combination of fixed and random effects, spatial autocorrelation of the site-specific random-effects coefficients would indicate the distances over which sites harbored groups more similar in size than expected by chance. Specifically, we expected that interconnectedness among local sites would be manifested in a spline correlogram by a drop in the correlation over a distance of a few tens of kilometers at most. Separate correlograms were calculated for the predisease winter of 1992–1993 and the postdisease winter of 2002–2003.

Detection Probability and Scope of Inference

Any observation of finches reflects a combination of biology (actual finch abundance) and the probability of detecting birds. Observer-induced biases are probably inherent in any single-observer counts of birds (e.g. Källander and Rydén 1974, Sauer et al. 1994, Bennetts et al. 1999). However, there are a number of reasons why we believe that the patterns identified here are the result of biological variation and are not sampling artifacts. First, we used paired-sample analyses in

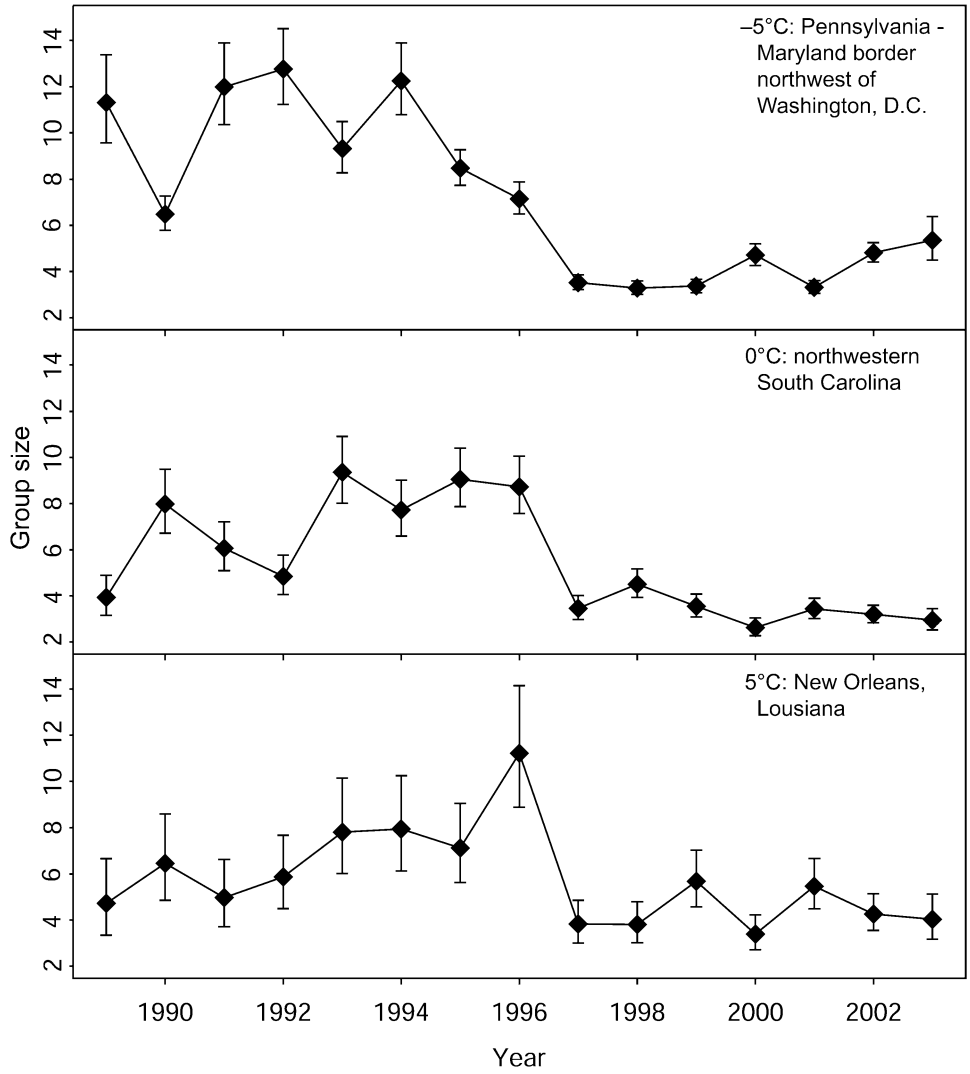

FIG. 2. Group sizes of House Finches declined during the establishment of *Mycoplasma gallisepticum* as a disease in this bird species between 1993 and 1996 and remained low subsequently. Estimated group sizes and confidence limits are predicted values for three arbitrary locations, chosen as the median latitude and longitude within each of three climatic bands that has a mean minimum monthly temperature within ±1°C of the temperatures indicated on the figure panels. Approximate descriptions of locations are given on the figure. The predicted values were calculated for December, suburban habitat, and with the maximum possible observer effort. December or January invariably were the months with the largest groups of House Finches reported at bird feeders, and suburban observers reporting the maximum observer effort are representative of a modal observer. The years on the *x*-axis are the calendar year from the second half of each winter.

the formal tests for determinants of severity in finch declines (Table 1), which eliminate most or all biases caused by intersite–interobserver differences. Second, counts of finches averaged across individual feeder sites reflect abundances over wider regions (Lepage and Francis 2002). Third, detection probability varies with observer effort, and all analyses explicitly included observer effort as a potential confounding variable; in all cases, higher observer effort clearly led to higher counts of finches. Large-scale differences in the readiness of finches to come to feeders would also have confounded the feeder counts of finches with the abundance of finches in an area. Again, we controlled for such effects by explicitly incorporating an index of

TABLE 1. Comparison of relative support (Akaike weight) for four predictors of magnitude of declines in group sizes of House Finches, from repeated-measures analysis. Regression coefficients for these predictors are also presented. Note that in the analyses of urbanization effects, no paired data were available from the most urban class.

Model	–2Ln (Likelihood)	AIC_C	ΔAIC_C	Akaike weight	Regression coefficient effect	Coefficient ± SE
Local predisease abundance	6,147.8	6,174.0	0	1	Local predisease finch abundance, 1993	0.02144 ± 0.00435
					Local predisease finch abundance, 2003	0.01910 ± 0.00394
Base model	6,264.0	6,286.1	112.1	4.55×10^{-25}		
Lowest monthly minimum temperature	6,263.5	6,287.6	113.6	2.10×10^{-25}	Minimum winter temperature, 1993	0.1974 ± 0.03909
					Minimum winter temperature, 2003	0.1893 ± 0.0313
Regional predisease abundance	6,266.5	6,290.6	116.6	4.65×10^{-26}	Regional predisease finch abundance, 1993	–0.5095 ± 0.1592
					Regional predisease finch abundance, 2003	0
Urbanization	6,267.8	6,298.0	124.0	1.16×10^{-27}	Rural, 1993	–1.4525 ± 0.8974
					Rural, 2003	–0.9220 ± 0.4344
					Semirural, 1993	1.0262 ± 0.7171
					Semirural, 2003	0.2832 ± 0.3578
					Suburban, 1993	0
					Suburban, 2003	0

regional abundance of finches as a predictor variable in all analyses. Similarly, finches' readiness to come to feeders could vary through the winter, with more finches coming to feeders during the coldest weather; seasonal variation in counts of finches was incorporated into our statistical models, and many analyses used a subset of the data from the period of highest reported group sizes of finches (mid-December to mid-January). Thus, we are confident that all major sources of variation in detection probability have been statistically modeled in our analyses.

Although we have controlled for variation in the probability of finches coming to feeders, we have not estimated these probabilities and separated the detection probability effects from variation in true sizes of local groups of finches. However, we do not believe that this is a problem in our system, because variation in probability of local finches coming to feeders, and thus variation in probability of detecting finches, carries a biological meaning in our study system. Finches are closely associated with humans in eastern North America, and in winter with bird feeders: finches are one of the 10 most prevalent bird species at feeders in much of our study region, being reported by >80% of participants in Project FeederWatch. Local studies in Ithaca (A. Dhondt et al. unpubl. data) suggest that finches come into their closest physical contact (thus increasing the likelihood of disease transmission) at or around bird feeders. Thus, fluctuations in numbers of finches observed at bird feeders are highly relevant to the question of whether finch sociality affects host–disease dynamics across wide geographic areas and through the winter season.

RESULTS

PATTERN OF AVERAGE GROUP SIZE DECLINES

In parallel with declines in overall abundance of finches (Hochachka and Dhondt 2000), group sizes declined and remained low following emergence and establishment of *M. gallisepticum* as a disease organism in finches (Fig. 2). At the colder, most northern site illustrated, these declines were from a relatively stable predisease level, whereas increasing group sizes with ongoing finch colonization and establishment were more typical of warmer and more southern areas prior to disease arrival. Note also that *M. gallisepticum* did not arrive in all locations simultaneously, which resulted in the differences in onset of decline shown in Figure 2. Although there have been some suggestions from FeederWatch data of increasing group sizes at the northern sample location in recent years, group sizes have remained below levels from the previous decade.

Only the time-course of declines from three specific locations are illustrated in Figure 2, but the declines occurred across the finches' eastern range in the United States (Fig. 3).

The statistical model used to describe single-year variation in finch group sizes appeared to be a good, but not perfect, descriptor of this variation. As noted above, confidence intervals around fixed-effect coefficients did not overlap zero, which indicates that the predictor variables influenced reported group sizes. Of the variation in group sizes that could not be explained by the fixed effects, the random effect of intersite differences did not explain the majority of this residual variance; in the two most intensively studied winters, consistent differences among sites explained only 24% (1992–1993 winter) and 46% (2002–2003 winter) of the random–residual variance. Sites with higher- and lower-than-average group sizes were not randomly distributed throughout the eastern United States. Visual inspection of random effects coefficients (Fig. 4) from the baseline Poisson regression analyses showed some large-area spatial structuring. For example, there were consistently smaller-than-expected (based on fixed effects) group sizes in the extreme northeastern (Maine) and southeastern (coastal Georgia) corners of the area examined, and consistently larger-than-expected group sizes in parts of the midwestern United States. Thus, although the fixed-effect predictor variables in our statistical models are able to account for much of the variation in group sizes of finches, there were still some inter-regional differences that could not be accounted for with our set of predictors. However, in both of the winters plotted (Fig. 4), ~50% of sites were within ±1 bird of the average expected group size, and ~75% were within ±1.5 birds of the expected.

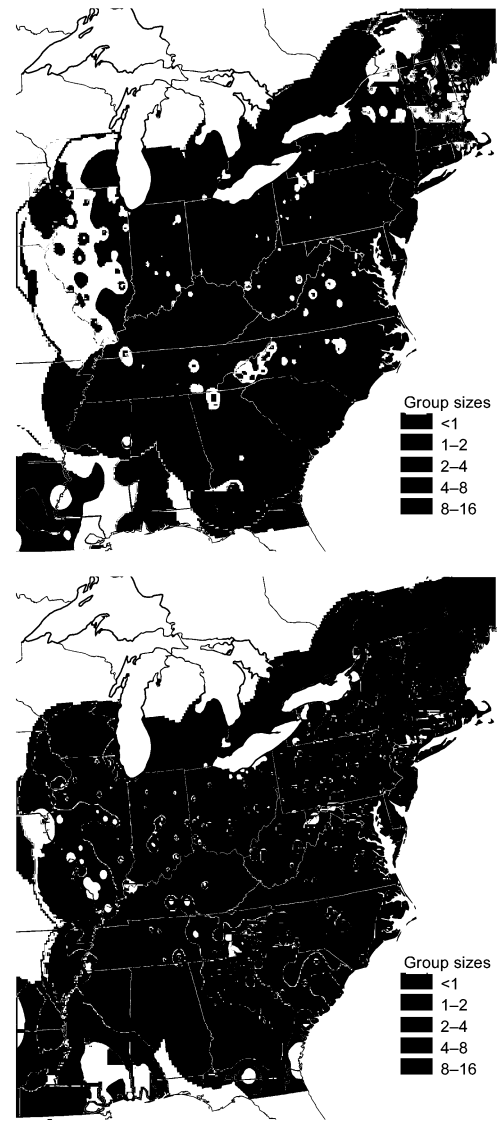

FIG. 3. Average group size was lower, and variation in group sizes through the House Finch's eastern range smaller, after establishment of *Mycoplasma gallisepticum* (bottom panel, 2002–2003 winter) than before the emergence of the disease organism (top panel, 1992–1993 winter). The maps present spatial interpolations (inverse distance weighted) from predicted House Finch group sizes at FeederWatch sites (Fig. 1). Interpolations are based on all available sites that reported between 16 December and 15 January of the winters in question, using only the single observation period closest to 1 January for each observer.

DID DISTRIBUTIONS OF FINCH GROUP SIZES CHANGE?

The illustrated declines in finch group sizes (Figs. 2 and 3) could have been caused by either a decrease in the modal group size or the disappearance of relatively large groups of finches. Both of these occurred, but the most dramatic change was the disappearance of large groups of finches (Fig. 5). There were, nevertheless, slight declines in modal group sizes along the entire gradient of urbanization, with the mode declining by ~1 bird after the emergence of *M.*

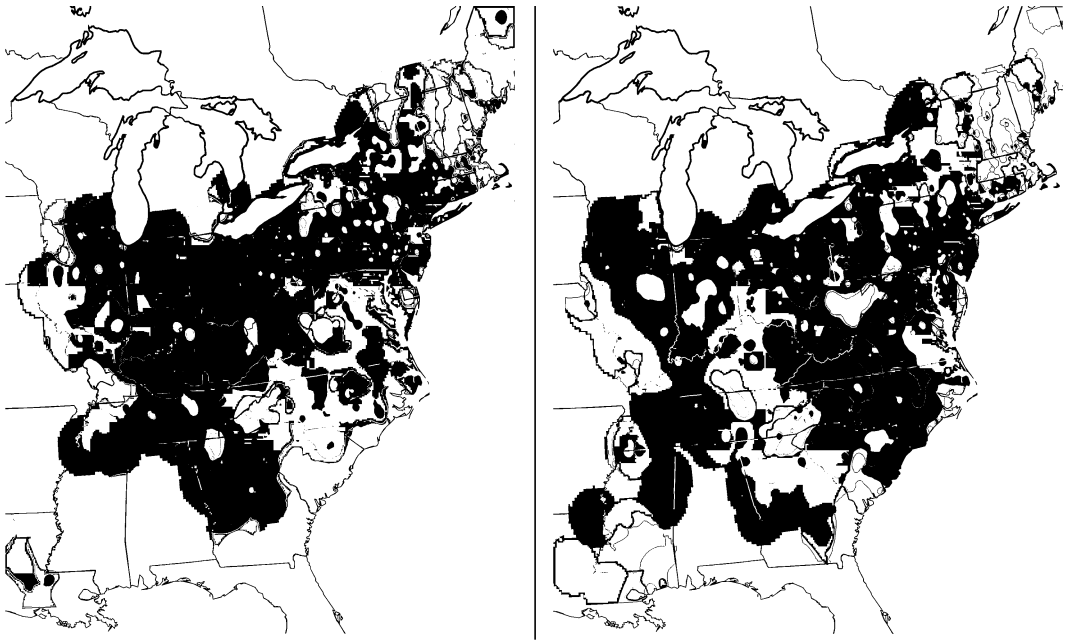

FIG. 4. Spatial distributions of random-effects coefficients describing site-specific deviations from average group sizes. Plotted are inverse-distance weighted interpolations from the random-effects coefficients for each site represented in the data in the 1992–1993 winter (left panel) and 2002–2003 winter (right panel). The middle gray tone—the dominant contiguous tone—represents sites whose average group sizes differed by <0.5 birds from the expected average group sizes. Black shading represents sites that consistently had group sizes of between one and three birds more than expected on the basis of average predicted values. The lightest gray shade indicates sites consistently hosting groups of between one and three fewer birds than expected. Large blocks of lighter or darker gray indicate regions whose sites typically had finch groups that were larger or smaller than expected on the basis of fixed-effect predictors in our statistical models.

gallisepticum as a disease organism in finches. To the extent that group sizes of finches are consistent at individual sites, these results suggest a disproportionate effect of disease at sites at which large groups of finches aggregated. This possibility is examined in more detail in the repeated-measures analyses described in the next section.

Identifying Predictors of Decline Rates for Finches

We more formally analyzed a subset of our data to identify factors that predict variation in the extent of the decline in group sizes, using paired-sample comparisons from 272 sites for which data were reported in both the 1992–1993 and the 2002–2003 winters. Only site-specific predisease abundance, of the four potential predictors examined, was well supported as a predictor of the size of declines in group size (Table 1). Almost 100% of support in the model set, judging from Akaike weights, was for the statistical model with the predisease site-specific group-size * year interaction. Sites with higher predisease group sizes showed the greatest declines. However, compensation was not perfect, and sites that had the largest group sizes before emergence of disease continued to have the largest group sizes (Fig. 6). As further indication that none of the other factors strongly affected the magnitude of declines in group size, the regression coefficients for the other effects all had standard errors that overlapped between the two winters contrasted in the interactions (Table 1).

Is There Spatial Autocorrelation in Abundance of Finches?

Site-specific differences in average group size were not the result of unidentified factors that caused local clusters of sites to have similar-sized

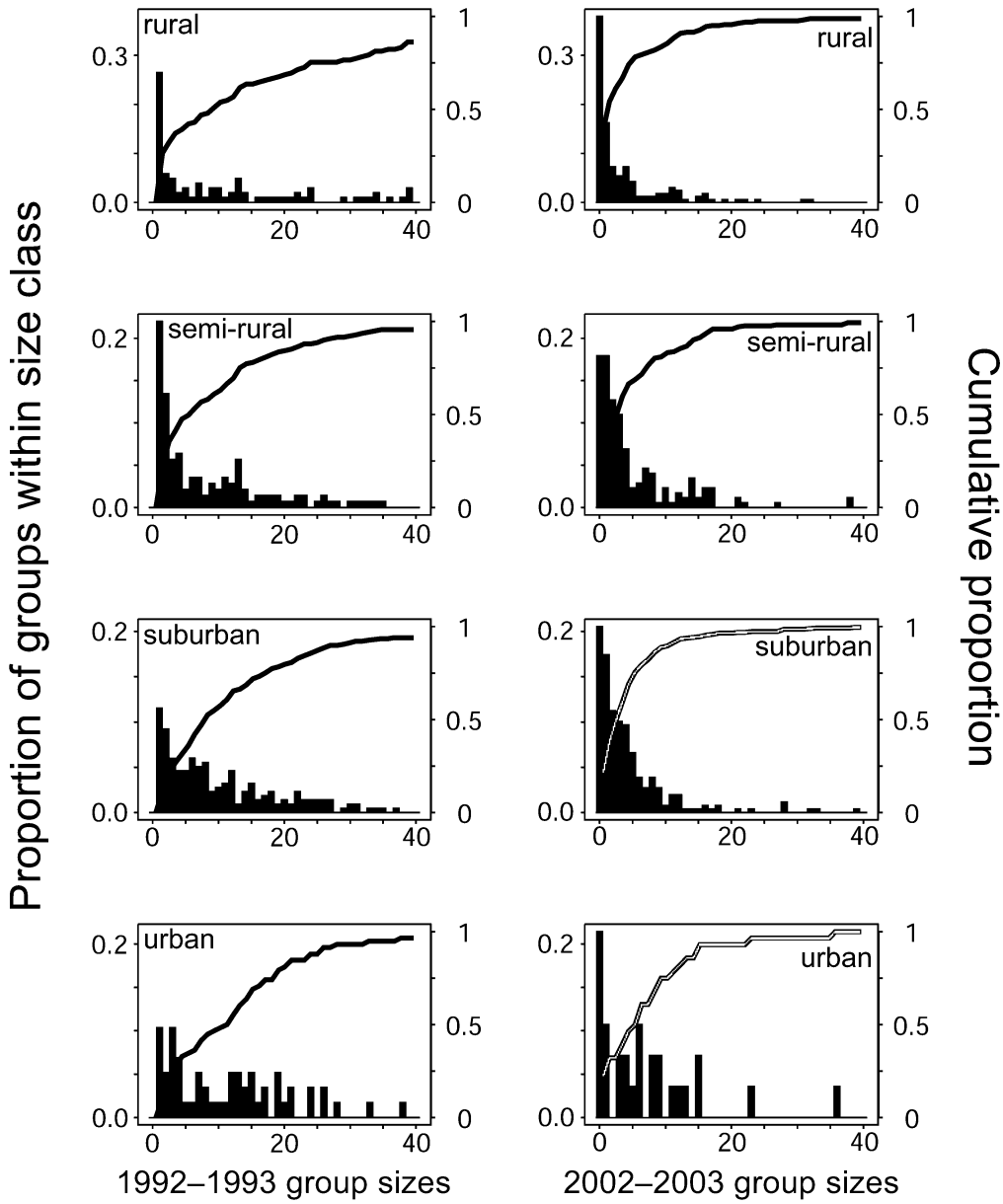

FIG. 5. The largest groups of House Finches were predominantly those that disappeared following the establishment of mycoplasmal conjunctivitis as a disease. This held true along the entire gradient of urbanization, across which average group sizes varied. Bars represent proportions of groups of a given size, and the gray lines are cumulative proportions. Note that in the 1992–1993 plots, cumulative distributions never reached 1, because the plotted distributions were arbitrarily truncated at 40 birds in all plots. Plotted values are predicted values from Poisson regressions, with a single data point from each site (closest date to 1 January), standardized to maximum observer effort. Because predicted values are plotted, noninteger group sizes are possible, such as the zero category that represents predicted group sizes of <1. To control for differences in predicted group size with overall abundance of House Finches in a region, we plotted only data from sites within ±1 bird of the median 5.2 birds per party-hour (CBC data for the 1992–1993 winter).

groups of finches. We reached this conclusion after calculating spline correlograms, which described the degree to which sites had similar consistent deviations from the average expected group sizes as a function of intersite distances (see above). Neither before nor after the establishment of *M. gallisepticum* was there any clear indication that nearby sites had groups of finches more similar in size than would be expected by chance alone (Fig. 7). This would have been indicated by spatial autocorrelations that decreased sharply as intersite distances increased out to a few tens of kilometers or less. Instead, we found gradual declines in similarity over distances of ≥300 km, which are likely the result of the regional clustering of higher- and lower-than-expected group sizes illustrated in Figure 4.

Discussion

The main pattern that emerged from our analyses was that group sizes, like regional abundance of finches (Hochachka and Dhondt 2000), declined (Fig. 3) and have remained low and relatively stable (Fig. 2) following establishment of *M. gallisepticum* in the finches. This average decline was caused, in part, by a small decline in the modal group sizes of finches, but to a larger extent because sites with the largest groups of finches no longer harbor very large groups, following establishment of the disease (Fig. 5).

This site-specific density-dependence in declines was borne out in our paired analyses of sites, given that only predisease group sizes at individual sites, of the four possible correlates that we examined, was related to the magnitude of decline of group sizes at individual sites (Table 1). We found no indication that severity of typical winter cold, pre-*Mycoplasma* regional abundance of finches, or the degree of urbanization, had any consistent effect on declines in group sizes. The lack of clear temperature effects is consistent with previous results from a local, intensive field study (Faustino et al. 2004), and lack of effect of regional variation in abundance is consistent with Altizer et al. (2004).

In keeping with the lack of effect of region-wide finch abundances on declines, combined

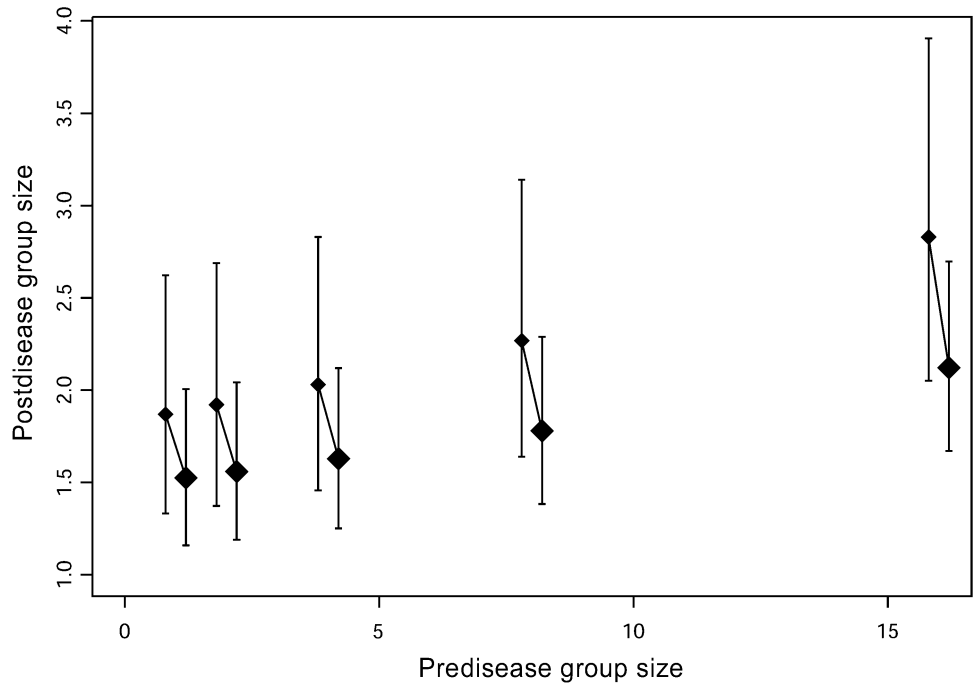

Fig. 6. Sites hosting larger group sizes of House Finches before the establishment of disease showed the greatest declines in group sizes, but nevertheless continued to report the largest groups of House Finches following disease establishment. Plotted are predicted values (for 1 January, with observer effort at its maximum) from paired-sample analyses with associated 95% confidence limits.

with existence of a local group size effect, was our failure to find high correlations in group sizes among nearby sites (Fig. 7). The spline correlograms showed that sites a few tens of kilometers apart were not more similar in group sizes than those 100–200 km apart. This pattern could indicate that site-specific characteristics cause birds to prefer some sites over others, even if individual birds range over relatively large areas. Alternatively, tight social groups with very restricted home ranges and little interchange among groups could cause our observed pattern (Fig. 7). Spread of disease outbreaks through space (e.g. during the initial *Mycoplasma* epizootic) depends on which of these alternatives was correct; variation in cohesion of social groups can alter host–disease dynamics (Wilson et al. 2003). Distinguishing between the alternatives for finches will require detailed local studies.

The observed density-dependence was not perfect, given that there is still variation in group sizes among sites (Fig. 5), with sites that harbored larger groups of finches before emergence of mycoplasmal conjunctivitis still tending to have larger groups following disease establishment (Fig. 6). This pattern could be the result of several phenomena, alone or in combination. First, if there is density-dependent variation in transmission of *M. gallisepticum*, the density-dependent response may not be linear (Barlow 2000), but instead may show

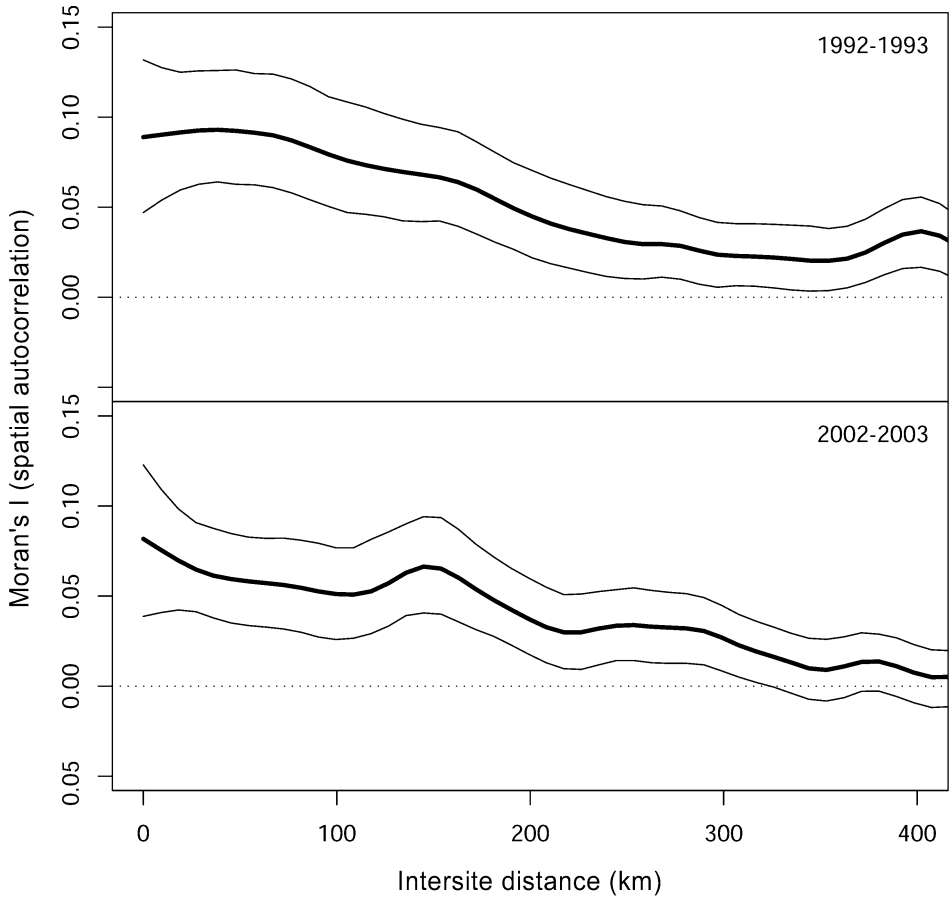

FIG. 7. There was no indication of unusually high spatial autocorrelation in group sizes of House Finches over short distances. Plotted are the predicted line and bootstrapped 95% confidence intervals around a spline correlogram. The spline correlograms were fitted to random-effects coefficients from the basic regression model used to describe patterns of variation in group sizes of House Finches.

accelerating transmission rates at higher finch densities and only act to reduce the sizes of the very largest groups. Second, density-dependent variation in severity of effects on infected birds—for example, if social stress varied with group sizes (e.g. Cheng et al. 2003)—may also have a nonlinear effect. Because our analyses of group size variation concentrates on the midwinter period after a typical peak in disease prevalence (Altizer et al. 2004), consistent year-to-year differences in site-specific abundance could be maintained if late-fall and early-winter aggregations at preferred sites were reduced by disease each winter. As a final alternative, birds at each location may be drawn from a different pool each winter and distribute themselves unequally on the basis of various decision rules (e.g. ideal free; Fretwell and Lucas 1970). Because the total pool has been reduced by disease, the current distribution may have changed such that extremely large groups no longer form, even at the most-preferred sites. Again, intensive local studies are needed to assess the relative importance of each of these possible mechanisms.

We see one biological conclusion emerging from our study: variation in the effect of disease on host populations can occur largely as a result of very local differences among environments. This contrasts with assumptions or findings from other studies (e.g. May and Anderson 1984, Grenfell et al. 2001, Smith et al. 2002) that there is substantial interconnectedness among local host populations and that host–disease dynamics depend on this interconnectedness. We base our conclusion on the findings that only site-specific variation in group sizes of finches were associated with magnitudes of declines in group sizes (Table 1 and Fig. 6) and that there was no evidence of higher-than-expected similarity in sizes among groups of finches at very nearby sites (Fig. 7). These results are somewhat surprising, given that in eastern North America, finches are partially migratory (Able and Belthoff 1998) and show different seasonal patterns of disease prevalence from north to south (Altizer et al. 2004). The ability of finches to move and spread disease quickly over long distances (see fig. 1 in Dhondt et al. 2005) and seasonal variation in disease prevalence are both likely related to disease transmission. So, potentially, our results, in juxtaposition with those of previous studies, indicate that local-scale influences on declines are largely the result of local site-to-site differences in mortality rates attributable to disease.

In addition to their biological implications, our analyses also illustrate the usefulness of analyzing large-scale "pattern" data for focusing more-detailed subsequent research.

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