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DISPERSAL, POPULATION GROWTH, AND THE ALLEE EFFECT: DYNAMICS OF THE HOUSE FINCH INVASION OF EASTERN NORTH AMERICA

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Abstract.—Since about 1940, when they were first released in the New York City area, house finches (*Carpodacus mexicanus*) have multiplied explosively and colonized much of eastern North America. We take advantage of the richly detailed documentation of this biological invasion to construct a mathematical model that predicts the rate of population spread on the basis of readily measurable demographic parameters. We seek to improve on previous models by predicting a rate of spread that accelerates following an initial period of slower growth, a pattern of spread followed by house finches as well as a variety of other invading species. We postulate that an Allee effect—disproportionately lowered fecundity below a critical threshold density of abundance—is the mechanism leading to a slower rate of spread in the early stages of the invasion. Our integrodifference equation model also emphasizes the link between long-distance dispersal and the rate of population spread.

Among the most notorious ecological invasions of North America are several that stem from the intentional release of birds such as the house sparrow (*Passer domesticus;* first introduced in 1853), the European starling (*Sturnus vulgaris;* first introduced in 1880), and the house finch (introduced in about 1940) (Long 1981; Hengeveld 1989). Researchers have repeatedly described these invasions but have attempted only a few quantitative analyses of their dynamics (Okubo 1986; Van den Bosch et al. 1992; Hengeveld 1994). Okubo (1986) used reaction-diffusion models to describe the spread of these three species but did not attempt to predict the rate of spread on the basis of individual behavior and demography. The approach of Van den Bosch et al. (1992) and Hengeveld (1994) was to use spatial age-structured integral models to incorporate demography and dispersal behavior in an analysis of the spread rates for European starlings, house sparrows, and other species.

The introduction and subsequent spread of the house finch in eastern North America provides an especially valuable opportunity for modeling by virtue of its comparatively recent occurrence. The process of population growth and spread was copiously documented through standardized surveys such as Christmas bird counts (CBC) and breeding bird surveys. Thousands of individuals were

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marked and hundreds recovered by banders, and a number of studies of basic reproductive biology were conducted within the eastern populations when they were expanding.

Our objective is to use the unique opportunity provided by the house finch invasion to construct an improved model for biological invasions that is strictly based on data for the distinct yearly reproduction and dispersal events. The mathematical formulation of this model is in terms of an age-structured integrodifference equation that describes discrete reproduction and dispersal events in a spatial continuum (see Kot 1992; M. Kot, M. A. Lewis, and P. van den Driessche, unpublished manuscript). The modeling framework also provides a natural way to incorporate data on significant but infrequent long-range dispersal events. The test of such a model should be in its ability to predict accurately the observed pattern of population spread—slow at first and then accelerating. Also important is the model's ability to link individual movement behavior (dispersal) realistically to the rate of population spread.

Central to analyses of spreading populations is an assessment of how individual movement behavior contributes to population spread. Movement behavior by birds is difficult to quantify, because birds commonly disperse at a spatial scale much larger than that encompassed by most study plots. Therefore, many past estimates of distances dispersed by birds tend to reflect the sampling pattern of recaptures rather than of the distances actually covered (Moore and Dolbeer 1989). We follow Moore and Dolbeer (1989) and Belthoff and Gauthreaux (1991) in using continent-wide band-recapture data to estimate dispersal by house finches. This method is comparatively unbiased, because of the more or less random spatial distribution of recovery effort. Beyond offering an improved description of the spread of house finches in eastern North America, we hope to provide an entirely new modeling approach for analyzing the spread of bird populations with discrete yearly reproduction and dispersal events and long-distance dispersal.

A critical component of our model is the incorporation of an Allee effect. This effect is a disproportionate reduction in reproduction below a threshold population density, due to the reduced probability that any individual will find a mate. It is a common observation that small and isolated populations of birds have low or even negative growth rates that often lead to extinction. Species of birds that have been successfully introduced to new areas have generally required repeated releases of large numbers of individuals (Long 1981). Furthermore, data on the early colonization by house finches in eastern North America show that observed breeding lagged behind first arrivals of pioneering individuals by 3–10 yr (see, e.g., Veit and Petersen 1993). This time lag suggests that early colonizers may not breed because they fail to find mates. Therefore, we assert that the inclusion of this effect within our model is reasonable and consistent with available data.

We carefully gathered data on house finches from a variety of sources to avoid the circularity of testing our model against the data that we used to construct the model in the first place. We estimated parameters for survivorship and fecundity from the literature and for dispersal from band recovery data. Since our model predicts the rate of spatial spread of the population, we compared the predictions of our model to population data extracted from Christmas bird counts. Thus, the data that we used to formulate the model were entirely distinct from those used to test it.

METHODS

House finches were introduced to Long Island, New York, in about 1940 (Elliot and Arbib 1953). Captive birds were apparently illegally released following a ban on their importation for the pet trade. It is not known exactly how many were initially released, but thousands were imported to the eastern United States from California in the 1930s and 1940s, and their New York City area population in 1951 was estimated at 280 individuals (Elliott and Arbib 1953). House finches proliferate in habitats modified by humans. They nest in ornamental plants in suburban backyards and forage in weedy fields and at bird feeders. They feed mainly (>90%) on weed seeds (Hill 1993). Between the time of their introduction and about 1960, their population grew, and their range spread to New Jersey and Connecticut. Beginning in about 1960, the rate of expansion of their range accelerated abruptly (figs. 1, 2*A*). The relationship between "range radius" (= the radius of a semicircle having the same area as the range encompassed by the house finch population) and time was linear from 1960 to 1970, slower during the 1970s, and then linear again from 1980 to 1990 (figs. 1, 2*A*). This pattern of spread corresponds to that of population growth within the core of the range (fig. 2*B*).

MODEL FOR BIRD DISPERSAL

Here we develop a model for bird reproductive dynamics, based on first principles and experimentally measurable parameters. Initially ignoring the dispersal process, we analyze the qualitative behavior of a population subject to these dynamics. We then include dispersal in adult and juvenile classes and derive a full integrodifference equation for the density of birds.

Bird Reproductive Dynamics

In modeling the dynamics for bird reproduction, our key assumption is density-dependent regulation of the population through competition for breeding sites. We also assume a 1:1 sex ratio and that males and females locate each other randomly and form pairs.

Our approach to modeling bird reproduction dynamics is as follows: First we determine the density of potential breeders in a given year t and location x. Next we use our model to determine the fraction of those potential breeders that actually form pairs. Finally, we determine what fraction of the potential breeding pairs produce offspring.

We denote $J_t(x)$ (juvenile density) as the density of birds that are 9–12 mo old in the spring of year t and $A_t(x)$ (adult density) as the density of birds that are more than 1 yr old in the spring of year t. The density of potential breeders in year t is thus $N_t(x) = A_t(x) + J_t(x)$.

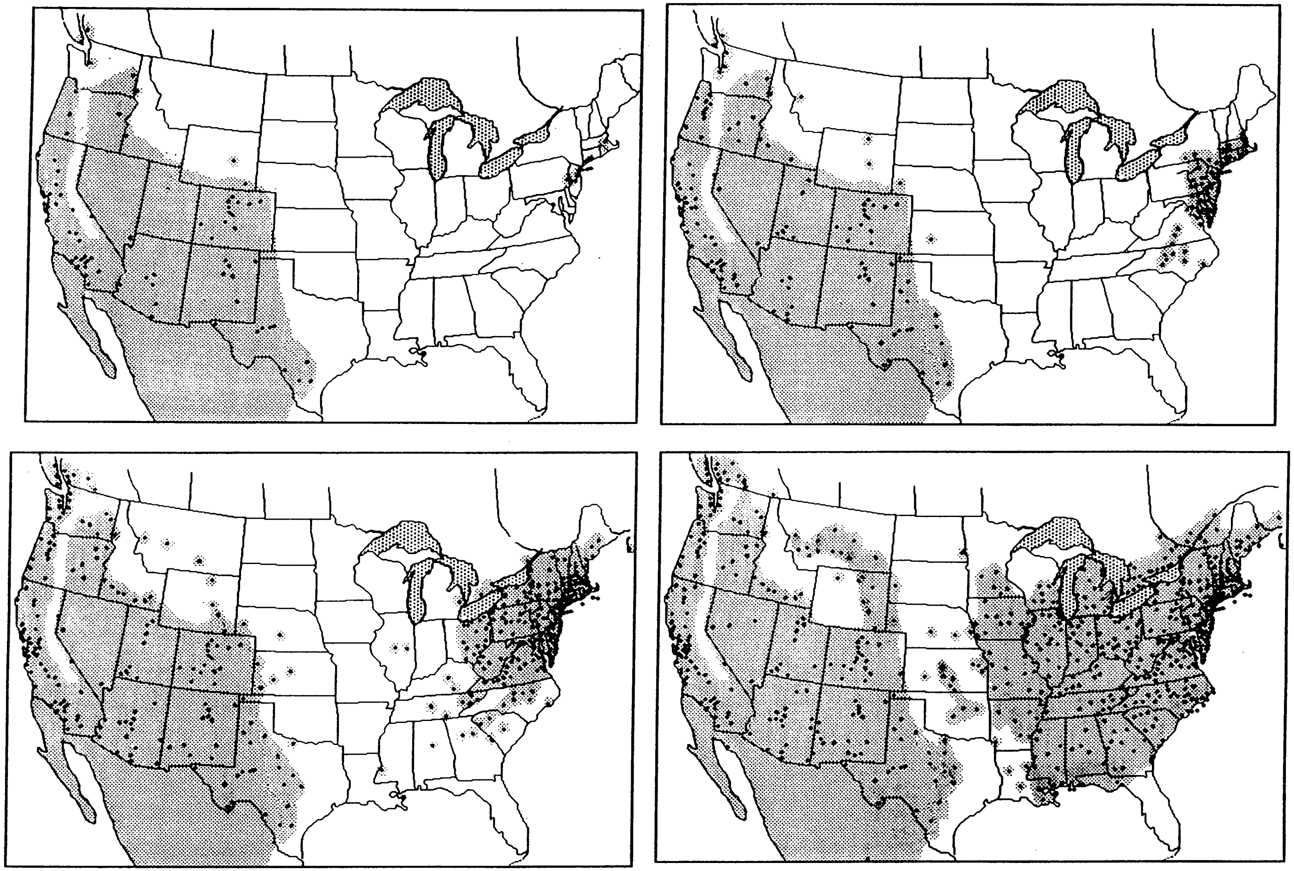

FIG. 1.—Spread of the house finch in North America. *Upper left,* 1958–1961; *lower left,* 1968–1971; *upper right,* 1978–1981; *lower right,* 1988–1990.

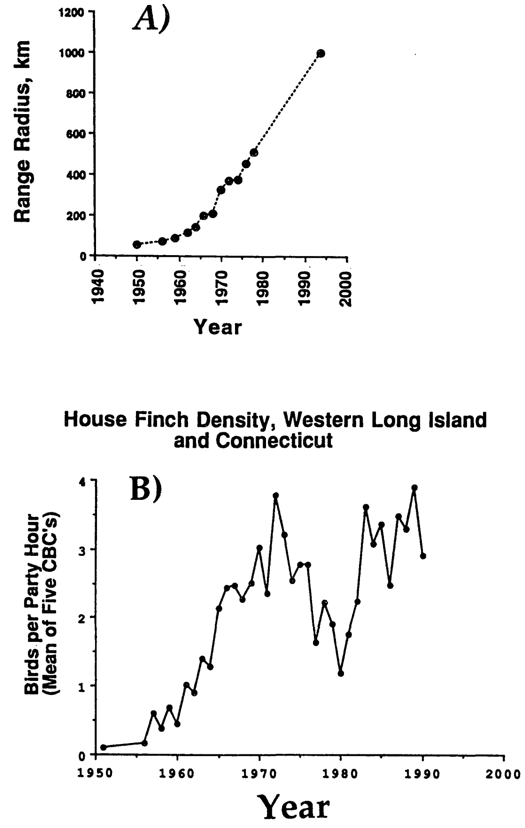

FIG. 2.—*A*, Spread of the house finch in North America. The range radius is calculated as the radius of a semicircle covering the area invaded from the Eastern seaboard. *B*, Mean number of house finches on five Christmas bird counts within the core area of their range. Number per square kilometer was estimated by dividing the total number counted by the area of a 15-mi-diameter circle.

Although the largest possible density of breeding pairs is $N_t(x)/2$, it is possible, and indeed likely, that not all potential breeders will form pairs. Random searching of males (M) and females (F) to form pairs (P) at a rate σ is modeled by

$$M + F \xrightarrow{\sigma} P\,. \tag{1}$$

Given a 1 : 1 sex ratio and applying the law of mass action, we have

$$\frac{dn}{d\tau} = -\frac{\sigma}{2}n^2, \quad n(0) = N_t \tag{2}$$

and

$$\frac{dP}{d\tau} = -\frac{1}{2}\frac{dn}{d\tau}, \quad P(0) = 0\,, \tag{3}$$

where $n(\tau) = M(\tau) + F(\tau)$, with the solution

$$P = \frac{N_t^2}{4/(\sigma\tau) + 2N_t}. \tag{4}$$

Given a fixed length of time, say, T, in which pair formation can occur, we have the density of pairs formed as

$$P(N_t) = \frac{N_t^2}{r + 2N_t}, \tag{5}$$

where $r = 4/(\sigma T)$ can be used to calculate the density of potential breeders that have not found mates as

$$n(T) = \frac{rN_t}{r + 2N_t}. \tag{6}$$

Note that as $T \to \infty$, $r \to 0$, the density of potential breeders that have not found mates approaches zero (eq. [6]), and the density of pairs formed approaches $N_t/2$ (eq. [5]).

Given a density $P(N_t)$ of potential breeding pairs, we assume that only a fraction $G(P)$ of them nest and breed successfully. With a finite density of nesting sites, the density of breeding pairs $H(P) = PG(P)$ must be bounded. Typical forms for density-dependent population regulation will have $H(P)$ as an increasing convex function of P, so that $H(P) \leq P$, $H'(P) > 0$, and $H''(P) < 0$. Note that these constraints coupled with equation (4) imply that H is an increasing function of N_t with a slope that is initially zero and an inflection point, which guarantees that $H(N_t) < N_t$ for small N_t.

A specific example is found by choosing H as the Beverton-Holt stock recruitment function (Clark 1990) normalized so that $H(P) \leq P$ for $P \geq 0$:

$$H = \frac{P}{1 + P/\delta}. \tag{7}$$

Here δ denotes the finite density of nesting sites available.

Finally, using equations (5)–(7), we find that the number of offspring born in year t and surviving to the end of their first summer is

$$cH(P[N_t]) = \frac{cN_t^2}{r + 2N_t + N_t^2/\delta} = f[N_t], \tag{8}$$

where c denotes the average number of offspring born to a breeding pair that survive the summer. This reproduction function exhibits critical depensation, or an Allee effect; low densities of potential breeders (N_t) result in a reduced per capita reproductive rate. The optimum population level for maximizing the per capita reproductive success, found by calculating the maximum of $H(P[N_t])/N_t$, is $N_t = \sqrt{r\delta}$ and yields

$$\frac{1}{2(1+\sqrt{r/\delta}} \tag{9}$$

successfully breeding pairs per potential breeder.

Ignoring dispersal for the time being and denoting s to be the probability that a juvenile or adult in year t will surve to year $t + 1$, we have the following equation:

$$N_{t+1} = sN_t + \frac{cN_t^2}{r + 2N_t + N_t^2/\delta}, \tag{10}$$

with steady-state solutions $N_{t+1} = N_t = N^*$ given by $N^* = 0$ and

$$N_{1,2}^* = \frac{1}{2}\left([c/(1-s) - 2]\delta \pm \{[c/(1-s) - 2]^2\delta^2 - 4\delta r\}^{1/2}\right) \tag{11}$$

if

$$\frac{c}{2(1+\sqrt{r/\delta}} > (1-s)\,. \tag{12}$$

In other words, the maximum per capita breeding rate must exceed the density-independent mortality rate for adults to have a positive steady-state solution (see eq. [9]). Linear stability analyses indicate that $N^* = N_1^*$ is unstable and $N^* = 0$ and $N^* = N_2^*$ are stable, and it can be shown using standard graphic methods that $N^* = 0$ attracts solutions starting below N_1^*, while $N^* = N_2^*$ attracts solutions starting above N_1^*. The steady-state N_1^* is thus the threshold below which the population will go extinct, and the steady-state N_2^* is the carrying capacity for the population at the end of the summer and before dispersal.

Including Dispersal

At the end of the first summer, some proportion p_J of the surviving offspring disperse, as does some proportion of the adult population p_A. Denoting the probability density function for the dispersal distance z of any given juvenile (a bird fledged during that year) as $\kappa_J(z)$, we describe the distribution of juveniles after dispersal by

$$J_t(x) = (1 - p_J)f[N_t(x)] + p_J \int_{-\infty}^{\infty} \kappa_J(|x-y|)f[N_t(y)]dy\,, \tag{13}$$

where x is the location of the bird after dispersal and y is the location of the bird before dispersal. In general, p_J may depend on N_t, so that the proportion of juveniles dispersing may be density dependent. Denoting the probability density function for the dispersal distance z of any given adult (a bird fledged in any year preceding the current one) as $\kappa_A(z)$, we describe the distribution of adults after dispersal by

$$A_t(x) = s(1 - p_A)N_t(x) + sp_A \int_{-\infty}^{\infty} \kappa_A(|x-y|)N_t(y)dy\,, \tag{14}$$

where s is the probabilitty that an adult will survive a year. In general, p_A may also depend on N_t so that the proportion of adults dispersing can be density dependent. Also, because each kernal $\kappa(z)$ is a probability density function, we have

$$\int_{-\infty}^{\infty} \kappa(z)\,dz = 1\,.$$

The exact shape of each kernel can be determined either empirically from the distribution of distances dispersed as measured from banding-recapture data as we do, or by construction based on explicit assumptions about bird movement (Neubert et al. 1995).

In the case of the house finch, release from Long Island meant that useful dispersal could not proceed in an easterly direction into the Atlantic Ocean. Under the assumption that during the dispersal stage there is no flux of dispersers to the east of Long Island, the dispersal kernel $\kappa(|x - y|)$ can be modified to the semi-infinite domain ($x \geq 0$, $y \geq 0$):

$$\kappa(x, y) = \kappa(|x - y|) + \kappa(|x + y|)\,. \tag{15}$$

Alternatively, use of this dispersal kernel on a semi-infinite domain is equivalent to use of the simpler dispersal kernel $\kappa(|x - y|)$ on an infinite domain with reflection symmetry imposed about $x = 0$. We use this latter approach in our numerical simulations.

Equations (13) and (14) can be added to yield a single equation,

$$\begin{aligned} N_{t+1}(x) = {} & s(1 - p_A)N_t(x) + (1 - p_J)f[N_t(x)] \\ & + \int_{-\infty}^{\infty} \kappa(|x - y|)sp_A N_t(y)\,dy + \int_{-\infty}^{\infty} \kappa(|x - y|)p_J f[N_t(y)]\,dy\,. \end{aligned} \tag{16}$$

This equation predicts the total density of adults and juveniles before the spring breeding ($N_{t+1}[x]$), based on the total density of adults and juveniles before the previous spring breeding ($N_t[x]$). Thus, $N_t(x)$ and $N_{t+1}(x)$ are effectively the expected density of birds at a Christmas bird count in successive years.

RESULTS

Reproduction and Survival

We estimated demographic parameters for the population dynamics (eq. [10]) from the literature. The mean number of offspring produced per pair equals 1.8–2.9. These values were taken from a study of 39 pairs of house finches breeding on Año Nuevo Island off central California (Hooge 1990). We were unable to find directly comparable data from eastern North America; however, Hill's (1993) estimates of 1.91 ± 2.01 young fledged per clutch in southeastern Michigan fall within the range of the California values. For the purposes of our numerical simulations, we assumed approximately two young were fledged per clutch and that each had a 75% chance of surviving the summer. Hence we chose $c = 1.5$.

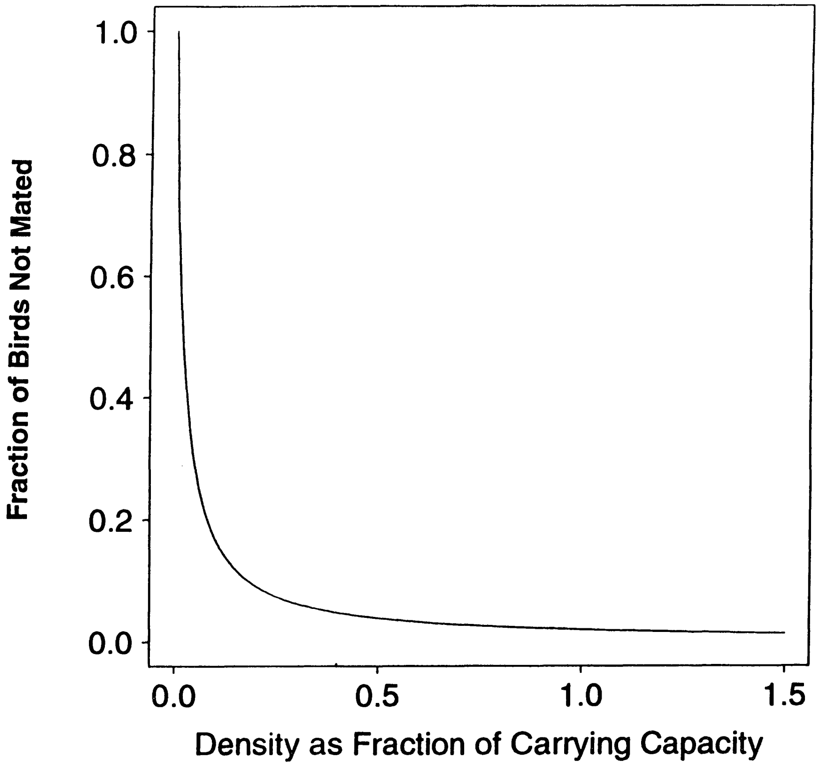

FIG. 3.—Fraction of unmated birds ($n[T]/N_t$; see eq. [6]) as a function of the fraction of the carrying capacity (N_t/N_2^*; see eq. [11]). Parameter values are $c = 1.5$, $s = 0.67$, $\delta = 1.5$, and $r = 0.15$.

Here we are using an average value; in the presence of double and even triple clutches, such as those observed in Michigan by Hill (1993), the value for c would be substantially higher than ours.

We used Milby and Wright's (1976) data, based on more than 800 banding recaptures from Kern County, California, to estimate annual survival of adults and juveniles. These values were 0.72 and 0.64, respectively. Hill (1993) gives a maximum Michigan life span of 11 yr, 7 mo, which is at least consistent with a probability of 0.02 of living 11 yr generated from the California survivorship values. We thus chose $s = 0.67$ in our simulations.

In the absence of accurate measurements of the Allee effect, we chose to assume that the majority of birds find mates, except when densities become very low. For example, a carrying capacity (N_2^*) of approximately 3.8 individuals per square kilometer and a weak Allee effect (4% of birds do not find mates at a density of half the carrying capacity [$N_2^*/2$]; see eq. [6]; fig. 3) yield parameters $\delta = 1.5$ and $r = 0.15$ from equation (11). With these parameters, the population growth function is as given in figure 4.

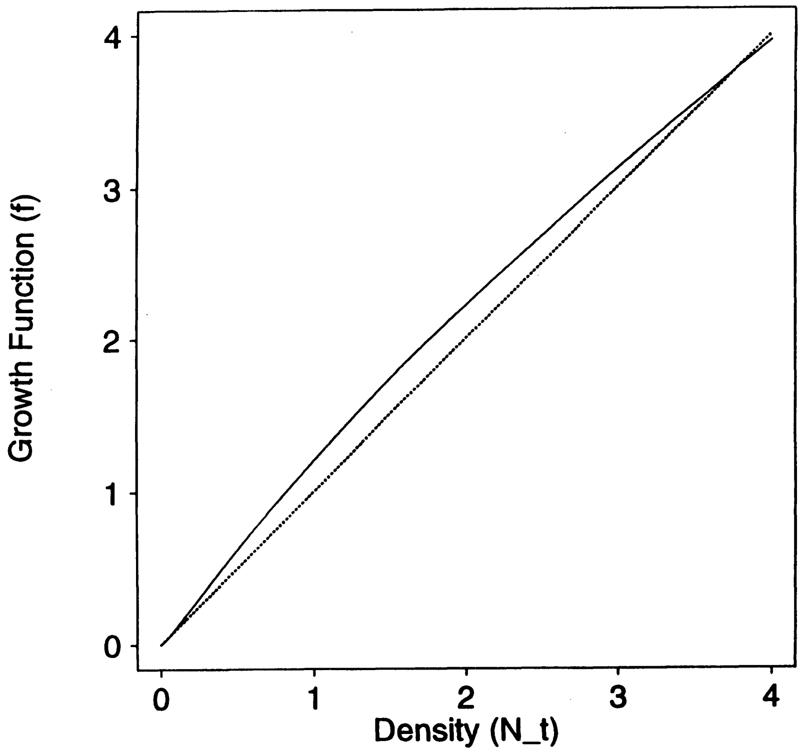

FIG. 4.—Growth dynamics given by equation (10). Parameter values are as given in figure 3.

Dispersal

We obtained from the United States Fish and Wildlife Service Bird Banding Laboratory all records of house finches banded in Massachusetts that were subsequently recaptured. We chose records from Massachusetts because of intensive efforts conducted in that state to band house finches during the 1960s and 1970s. Of the more than 8,000 finches banded between 1960 and 1990, there were 45 individuals trapped within their "hatching year" (<9 mo old) that were subsequently retrapped and 27 recaptures of "after hatching year" individuals (>12 mo old). We constructed frequency distributions of the distances dispersed and then fitted a modified Weibull function to the frequency distributions using maximum-likelihood estimation with SYSTAT (Hastings and Peacock 1986; Wilkinson 1988). Finally, we scaled the function to yield a probability density function integrating to unity:

$$\kappa(z) = \frac{a}{2b\Gamma(1/a)} \exp\left[-\left(\frac{z}{b}\right)^{a} \right]. \tag{17}$$

The values for a and b calculated for the juvenile and adult dispersers were $a_J = 0.468$, $b_J = 41.056$ km, $a_A = 0.859$, and $b_A = 76.893$ km. The mean dispersal

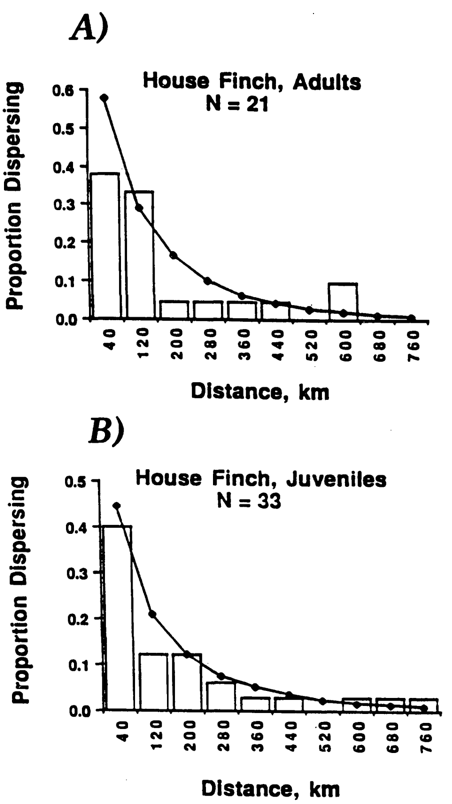

FIG. 5.—*A*, Frequency distribution of dispersal distances for adult house finches from Massachusetts; *B*, dispersal distances for young-of-the-year house finches.

distances calculated from the fitted distribution, using $M = b\Gamma(2/a)/\Gamma(1/a)$, were $M_J = 329.28$ km and $M_A = 98.29$ km. The fitted functions are compared with the data in figure 5. Of the 72 recaptures that we analyzed, 12/45 (27%) of the juveniles and 6/27 (22%) of the adults did not disperse at all; that is, they were recaptured at the same place where they had been originally banded.

These values are comparable to others that have been calculated for eastern North American house finches. For example, Belthoff and Gauthreaux (1991) analyzed 333 banding recaptures from throughout eastern North America and found that 27.8% of males and 20.9% of the females (not segregated by age) were recaptured where they had been banded. They also reported a mean dispersal distance of 109.3 km (this value was recalculated from their graph). Stewart (1989) analyzed 455 recaptures from New York and Pennsylvania and reported proportions of individuals not dispersing ranging from 18.3% to 26.2%. Stewart did not report mean or median dispersal distances but did list maximum distances dispersed of 900 and 1,200 km, both substantially larger than the 700 km from the Massachusetts data. In sum, there is substantial agreement in distances dispersed by house finches among the various sources of data that we were able to extract from the literature.

It is important for the purposes of our model to demonstrate that house finches disperse individually rather than in flocks. If house finches dispersed in flocks, then it would be difficult to argue that an Allee effect was important because the pairs would already be together upon arrival. We ascertained that house finches disperse individually by searching the literature for the earliest records of occurrence in a variety of eastern states. Compilations of records were available for New Jersey (Leck 1984), Massachusetts (Veit and Petersen 1993), Vermont (Laughlin and Kibbe 1985), Arkansas (James and Neal 1986), Iowa (Dinsmore et al. 1988), Illinois (Mumford and Keller 1984), and Indiana (Bohlen 1989). Of 17 records of early colonists found in these states, 15 were of single birds, and the last two occurred together as a pair. These data show that house finches disperse individually, at least along the outer fringes of the population. Furthermore, there was a lag of 3–10 yr between the first record of occurrence of a house finch in a state and the first recorded instance of breeding. This pattern strongly suggests that early colonists do not breed because there are no mates available. This condition is the essence of the Allee effect.

We assumed that the proportions of juveniles and adults dispersing, p_{J} and p_{A}, respectively, increased monotonically with the local population density. In the absence of exact data, we assumed that $p_{\mathrm{J}} = p_{\mathrm{A}} = p$, for the following piecewise linear function:

$$p(N_t) = \begin{cases} \dfrac{N_t}{N_2^*} & \text{if } N_t < N_2^* \\ 1 & \text{otherwise} \end{cases} \tag{18}$$

(fig. 6). The notion that probability of dispersal should be related to increasing population density in this way is supported by an analysis (R. R. Veit, unpublished manuscript) of long-distance dispersal in the yellow-headed blackbird (*Xanthocephalus xanthocephalus*). In that species, incidence of dispersal to the Atlantic Coast from its western breeding range was found to be significantly related to estimated breeding success during the same year. That is, following summers during which large numbers of young were produced, large numbers of young were found at the Atlantic Coast during fall.

Initial Distribution of Finches

Because the initial release of house finches is presumed to have been by bird dealers responding to a ban on the sale of house finches in April 1940 (Elliot and Arbib 1953), there are no data on the number released. For the purposes of our numerical simulations, we assumed that, immediately after release, the initial range covered a semicircle with a 10-km radius and a density of 0.5 individuals per square kilometer. This approach gives the total number released as approximately 80 finches.

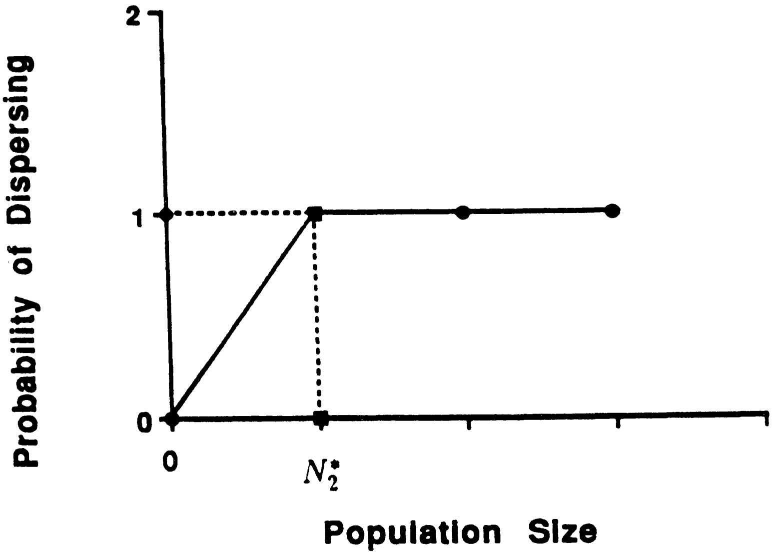

FIG. 6.—Density-dependent dispersal proportion (see eq. [18])

Model Results

Our model predicts an abrupt acceleration of population growth and spread following an initial period during which these rates are much lower. This pattern is shown clearly by the CBC data on house finches from the New York City area, as well as on more broad-scale analyses (Okubo 1986). With our simulations, we will show how the inclusion of an Allee effect coupled with density-dependent dispersal leads to the initial period of slow growth during the years 1940–1960.

Numerical Simulations

The model equations are derived for use on an infinite spatial domain. However, within our numerical simulations, we used a finite domain but chose a spatial domain sufficiently large and a temporal domain sufficiently small to prevent the solutions from exhibiting boundary effects. Rather than solving the full two-dimensional problem numerically, we solved the equivalent one-dimensional problem represented by equations (8), (16), and (17) with initial conditions symmetric about the point $x = 0$, on the domain $-1{,}500 \text{ km} \leq x \leq 1{,}500 \text{ km}$. This approach is equivalent to solving equations (8), (15), and (16) on the domain $0 \text{ km} \leq x \leq 1{,}500 \text{ km}$. The switch from a two- to a one-dimensional problem introduces some error, particularly early in the invasion process when the invading front is not planar. However, this error would simply tend to deemphasize the slowness of early spread (Lewis and Kareiva 1993). Thus, slow, early spread would be even more apparent in the equivalent two-dimensional model, and our formulation errs on the side of being conservative when explaining the initial slow and then accelerating spread rates.

A numerical solution of equations (10), (16), (17), and (18) with the parameters

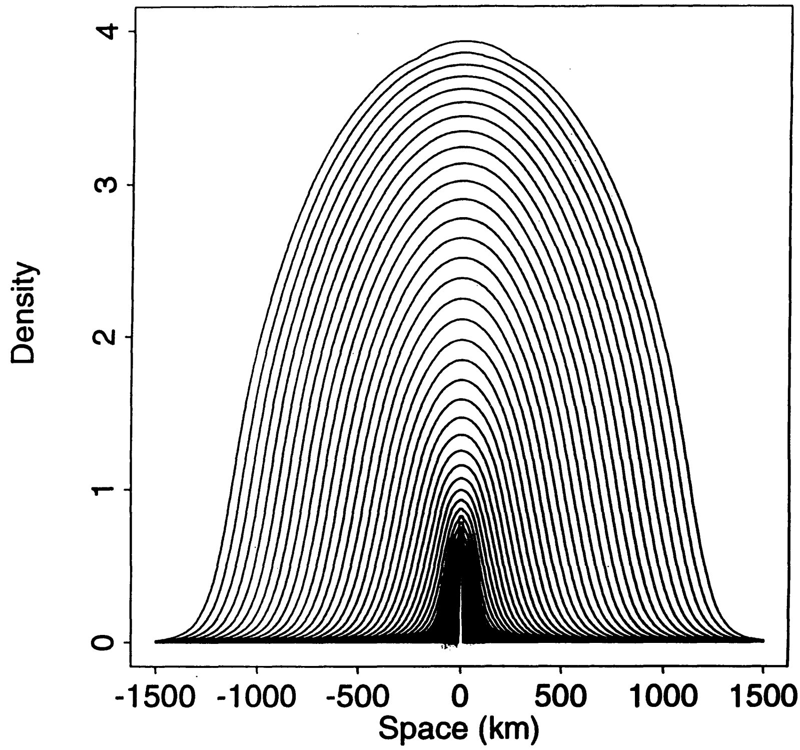

FIG. 7.—Numerical solution of the integrodifference equation defined by equations (10), (16), (17), and (18) with initial conditions as described under *Initial Distribution of Finches* and parameter values of $c = 1.5$, $s = 0.67$, $\delta = 1.5$, and $r = 0.15$.

and initial data as given above is shown in figure 7. The range, specified by the distance at which the density reaches a threshold of 0.1 bird per square kilometer, is given in figure 8*A*, and the density of finches at the center of the range ($x = 0$) is given in figure 8*B*. Note the positive correlation between the range and density at the center of the range. During the last 20 yr (years 30–50), the bird front moved approximately 800 km, giving a spread rate of approximately 40 km per year. From the CBC data on house finch abundance in the New York City area (fig. 2*B*), it is evident that growth was strongly positive through the 1960s, then negative in the 1970s, then once again strongly positive in the 1980s. These fluctuations in population size within the core of the range correspond closely to the rate of expansion of the population. The rate of increase of the range radius was slowest during the 1970s, the time when population growth in the center of the range was negative.

Figure 9 shows that our Allee threshold of 0.15, which was interpolated from the core area CBC data, yields a better prediction of the rate of population spread than do values of 0.05 or 0.25. Were this effect to approach zero, meaning that population density could never be so low as to limit reproduction, the depressed

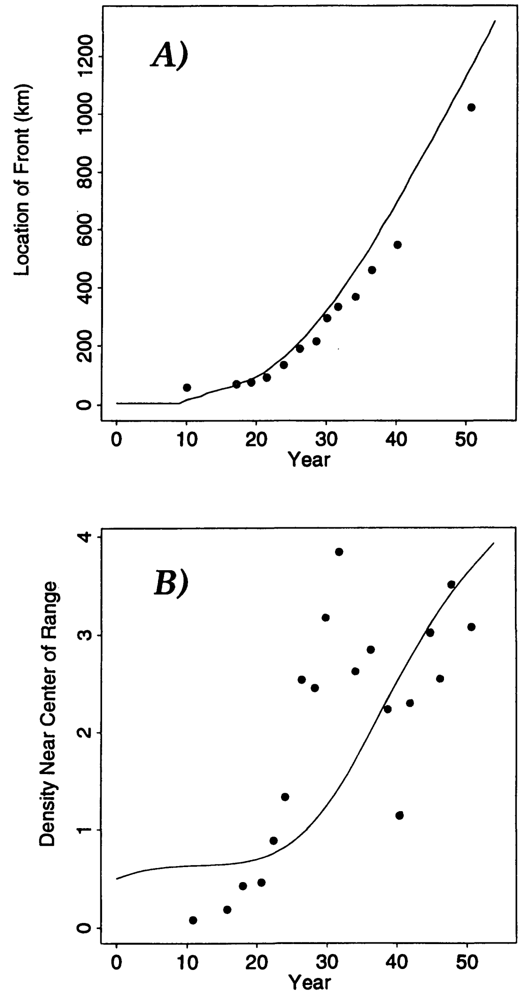

FIG. 8.—*A*, Range of population spread for the numerical solution described in figure 7 with a detection threshold of 0.1. The data shown in figure 2*A* are superimposed. *B*, Density at center of range ($x = 0$) for the numerical solution described in figure 7. The data shown in figure 2*B* are superimposed.

initial rate of spread so characteristic of invasive populations would not be evident.

DISCUSSION

We have formulated a model that faithfully recounts the spread of the house finch population in eastern North America, based on independent estimates of life-history parameters that we thought were most relevant to the invasion process. Taking the form of an integrodifference equation, the model incorporates

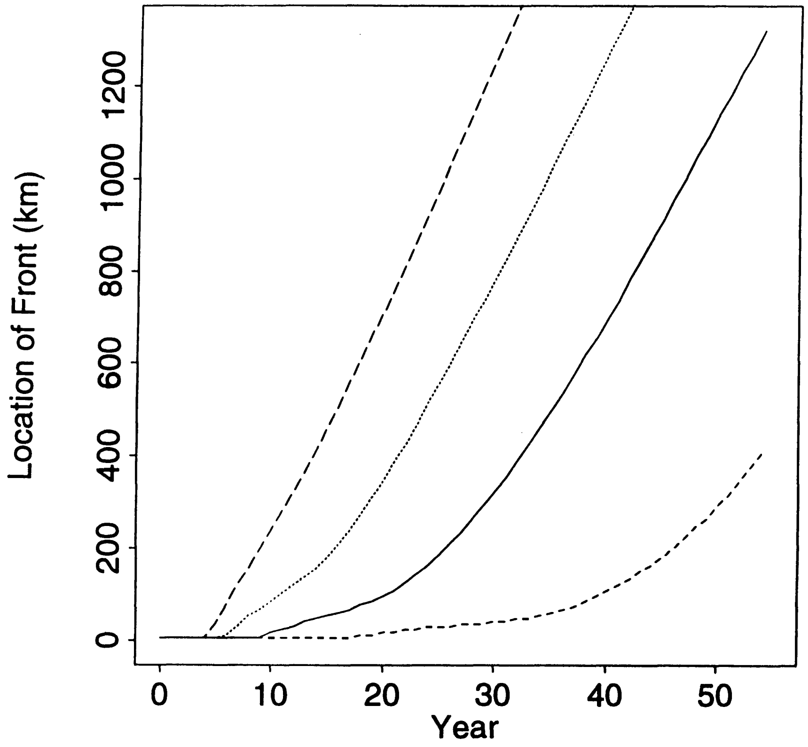

FIG. 9.—Range of population spread for the numerical solution described in figure 7 but with $r = 0$ (*upper dashed line*), $r = 0.05$ (*dotted line*), $r = 0.15$ (*solid line*), and $r = 0.25$ (*lower dashed line*).

distinct growth and dispersal phases and includes an Allee effect (critical depensation) in the growth dynamics. We suggest that the model may have a broad application to a variety of species, because its parameters relate to general biological attributes, and the actual parameter values, such as growth rates and dispersal distances, can be individually tailored.

Our approach differs from related efforts to model similar data in the kind of model we use. We assert that the integrodifference equation is fundamentally suited to modeling bird growth and dispersal because the underlying structure of both the equation and the biology is of discrete reproductive events interspersed with large-scale dispersal events. Thus, every component of the model is tied closely to the related biology. In an attempt to produce as realistic a model as possible, we have also included factors often left out of previous models. These are density-dependent dispersal and disproportionately lowered reproductive success below some threshold population density (Allee effect). Although analytical tools can be used to determine invasion rates via traveling wave solutions (Kot 1992; M. Kot, M. A. Lewis, and P. van den Driessche, unpublished manuscript), our approach to analyzing the model is numerical, primarily because we have sacrificed simplicity of formulation for biological realism.

The model explains two key features of the data: an initially slow, then abruptly accelerating rate of population spread, which eventually reaches an asymptotic invasion velocity; and a strong correlation between the rate of population spread and the rate of population growth near the center of the range. Numerical simulations for a variety of parameter values showed that the Allee effect dramatically slowed the population spread rate, especially the early spread (Lewis and Kareiva 1993; Kot et al. 1995), and that the nonlinear dispersal increased the length of time taken before the invasion achieved an asymptotic constant spread rate. The actual rate of spread of the house finch population was underpredicted by our model for the first 10 yr after release and slightly overpredicted thereafter. Given the simplifications we have made in the modeling process, we argue that the fit of the data to our theoretical prediction is as good as one might reasonably expect.

The first feature is hardly unique to house finches. Hengeveld (1989) shows that an acceleration of the rate of spread after a period of slow initial growth is characteristic of organisms as diverse as the red deer and Himalayan thar (*Hemitragus jemlahicus*) in New Zealand, the Japanese beetle (*Popillia japonica*) and starling in North America, and the collared dove (*Streptopelia decaocto*) in Europe. Perhaps the best evidence in support of the biological plausibility of an Allee effect is the history of introductions of nonnative birds into North America. Using data in Long (1981), we counted 74 species of nonindigenous birds that have been introduced into North America, many of these species repeatedly and in substantial numbers (more than 1,000 individuals). Of these 74 species, 28 have persisted long enough that we can be confident that they have been reproducing in the wild. Of these 28 introduced species that have persisted, only nine species (mute swan, *Cygnus olor;* chukar, *Alectoris chukar;* European partridge, *Perdix perdix;* ring-necked pheasant, *Phasianus colchicus;* rock dove, *Columbia livia;* collared turtledove; monk parakeet, *Myiopsitta monachus;* starling; and house sparrow) have spread more than 20 mi from the point of introduction. Of the species that have persisted but not spread, almost all have been continuously present at very low population densities, mainly in southern California and Florida. Those species that have persisted in California and Florida have been limited by something other than "warm" climates; their populations have been limited to tiny subdivisions of each of these states. The species that have spread, on the other hand (with the possible exception of monk parakeet), have been repeatedly reintroduced and had achieved large (at least hundreds of individuals) populations before spreading.

We cannot prove what mechanism has prevented the spread of these populations, but a reduced population growth rate at low densities seems an eminently reasonable hypothesis. Alternative models that we explored that ignored either an Allee effect or density-dependent disperal did not yield qualitatively correct behavior over a range of reasonable parameters.

Mundinger and Hope (1982) propose that the population spread of the house finch involved a combination of long-range "jump" dispersal and short-range diffusive movement. Maps of the spread of the house finch population show evidence of such "jumps"—isolated patches of house finches seemingly becoming established ahead of the advancing front of the population. This pattern is not inconsistent with our model predictions. Since the model disperses birds according to the frequency distributions of band recoveries, individual house finches do become isolated by virtue of dispersing hundreds of kilometers farther than "average." These jumps are included in the tails of the dispersal kernel. That such patchiness is not evident in the model output is due to the fact that the model is deterministic, predicting the expected density of birds at a given distance. (See, e.g., Minogue 1989 for a discussion of stochastic aspects of spatial spread.) Furthermore, the addition of normal spatial variation in growth rates would also tend to increase the patchiness of the final predictions.

Our model differs subtly from that formulated by Van den Bosch et al. (1990, 1992) in the way that dispersal is characterized. They use the statistical characteristics of a Gaussian distribution to quantify the outward spread of a population; that is, dispersal is portrayed as a bell-shaped curve that collapses as time elapses. Our approach is more direct in that we have fitted a function to a frequency distribution of distances taken directly from data. Our model ignores the mechanism by which birds achieve the observed spatial redistributions and does not assume random motion. Van den Bosch et al. (1992) also assume that individuals settled permanently following dispersal during their first year of life. Our band recovery data for house finches show that house finches continue to disperse as adults, and this finding is consistent with Moore and Dolbeer's (1989) analysis of blackbird dispersal. Since dispersal distances by birds have rarely been estimated using band-recovery data of known-age birds, we suggest that dispersal of birds older than 1 yr is likely more common than generally believed.

We suspect that part of the reason that a model for bird spread such as the one we present has not been formulated in the past is that previous estimates of bird dispersal distances have been too low to account for observed rates of population spread. Many ornithologists will be surprised that individual house finches travel as far as 700 km within a single year, because such large dispersal distances have in the past been almost impossible to measure. Moore and Dolbeer (1989) have shown, through an exhaustive analysis of banding recoveries of blackbirds, that previous estimates of dispersal distances of blackbirds have been too low by a factor of 10–100. Since our model, which is based on dispersal data collected in the same fashion as Moore and Dolbeer's, predicts rates of population spread that are in accord with observations, we believe that we have captured some of the biology most pertinent to the analysis of biological invasions.

An important characteristic of the dispersal process is somewhat obscured by the format of our data presentation. Because of the skewed distribution of distances dispersed by individual house finches, each year our model will fling out individual house finches considerable distances (100–300 km) ahead of the main front of the advancing population. Therefore, a map of all individual house finches during any given year would reveal isolated individuals distributed outside an arbitrary contour encompassing most of the population. Since our model results are shown as expected densities over spatial domain, isolated individuals are not evident. We emphasize that there is no inconsistency between our simulation results and the "real" pattern of population spread by birds, which is characterized by the appearance of isolated individuals far beyond what may arbitrarily be defined as the species range.

As our model makes a prediction of the rate of population spread based on independently derived estimates of individual dispersal rates, it suggests that it may have applications to biological invasions in general. The data and numerical solutions shown in figure 8 indicate the model adequately predicts both the qualitative nature and velocity of the spread (approximately 40 km/yr) and the density of birds near the center of the range as a function of time.

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