Vagrants as the Expanding Fringe of a Growing Population

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Models of invasions have revealed the importance of rare, long-distance movement to the rate of population spread (Kot et al. 1996, Veit and Lewis 1996, Lewis 1997). For example, the rate at which House Finches (*Carpodacus mexicanus*) spread throughout eastern North America beginning in the 1950s was driven by the small proportion of the population (ca.10%) that moved farther than 500 km, or about 10 times the average distance (Veit and Lewis 1996). The evidence from House Finches suggests that vagrants are simply the individuals that make up the long tails of leptokurtic frequency distributions typical of data on distances moved by animals (Hengeveld 1989). Vagrants can contribute disproportionately to the genetic makeup of populations that they join by virtue of their distant origin and consequent genetic dissimilarity (Wright 1943).

It is difficult to quantify long-distance movement of birds because of the large distances involved. Even nationally coordinated banding studies have been hampered by small samples and biased recapture distributions. But a vast and largely untapped body of information is available in the form of records of vagrant birds (DeSante 1983, Patten and Marantz 1996, Veit 1997). Vagrants are individuals that disperse far (farther than 90% of the population; Veit and Lewis 1996). Thus, they are linked to population growth in the way specified by the integro-difference equations of Kot et al. (1996), Veit and Lewis (1996), and Lewis (1997). Large numbers of vagrants in any given year result from the production of large numbers of young. If a link between vagrancy and reproduction can be supported, then records of vagrant birds will prove to be an especially useful tool in the modeling of avian population dynamics (Johnson 1994).

Estimates of persistence time of threatened populations are contingent upon accurate estimates of dispersal distances. In theory, the probability that an individual will disperse, and the distance traveled by dispersers, can have profound effects upon population trajectories (Bascompte and Sole 1994, Hassell et al. 1995, Ruxton 1996, Ruxton et al. 1997). For example, estimates of population persistence in Spotted Owls (*Strix occidentalis*) depend critically upon estimates of the likelihood that a young owl disperses and the distance that dispersing individuals move (Lamberson et al. 1993).

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My objective is to extend an analysis of long-distance dispersal in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Veit 1997) to other species to provide further support for the link between vagrancy and population growth. I estimated the correlation between the annual occurrence in Massachusetts of five western North American passerines (including Yellow-headed Blackbird) and breeding success estimated by the Breeding Bird Survey (BBS; Robbins et al. 1986, Sauer and Droege 1990). I determined whether vagrancy to Massachusetts was correlated with increased reproduction within some portion of the breeding range. That is, as in Veit (1997), I postulated that movement behavior does not vary much between years and that large numbers of vagrants are the consequence of large numbers of young being produced.

Data on vagrants, and data on reproduction based on BBS, are not without limitations. Nevertheless, these data provide the only current opportunity to study long-distance movement and growth of bird populations on a continent-wide scale. The potential usefulness of these data justifies exploratory analysis.

Methods.—Data on vagrant passerines were collected from records maintained at the Massachusetts Audubon Society. I selected the species for analysis based on their frequency of occurrence in Massachusetts. Western North American passerines that occurred with a mean of at least five individuals per autumn from 1966 to 1988 were included. The five species that met these criteria were Western Kingbird (*Tyrannus verticalis*), Western Tanager (*Piranga ludoviciana*), Clay-colored Sparrow (*Spizella pallida*), Lark Sparrow (*Chondestes grammacus*), and Yellow-headed Blackbird. The methods for counting individual vagrants appearing in Massachusetts are described in Veit (1997).

I used the BBS "Indices of Annual Abundance" from 1966 to 1988 (Sauer and Droege 1990). My objective was to test whether the number of vagrants appearing in Massachusetts during a given fall was related to the number of young produced within the breeding range during the preceding summer. I estimated the correlation between vagrants in Massachusetts in year t and breeding abundance in year $t + 1$ under the premise that abundance in year $t + 1$ is an index of reproduction in year t. The annual indices were calculated at three spatial scales: (1) continent wide; (2) one-third of the continent (eastern, central, and western North America); and (3) ecolog-

TABLE 1. Correlation between vagrancy in Massachusetts and population growth within Breeding Bird Survey (BBS) strata for five passerines from western North America.

Species	Strata[a]	r_s	n	P	Vagrancy[b]
Western Kingbird	34 (S34)	0.42	23	0.02	7
Western Tanager	19 (S84)	0.36	22	0.05	5
Clay-colored Sparrow	12 (S64)	0.51	21	0.01	3
Lark Sparrow	37 (S31)	0.55	23	0.004	7
Yellow-headed Blackbird	24 (S30)	0.50	23	0.007	3

[a] Number of strata in which species breeds based on BBS data; numbers in parentheses identify strata for which the highest correlations were achieved.

[b] Number of strata for which abundance was correlated ($P < 0.1$) with vagrancy in Massachusetts.

ical strata, of which there are 99 in North America (Robbins et al. 1986, Sauer and Droege 1990).

I calculated Spearman rank correlation coefficients between the 23-year time series of vagrants in Massachusetts and the BBS data. I used rank correlation coefficients because I was interested in whether the years with the most vagrants were, on average, the same as the years with the greatest increase in population size.

Results.—For two species out of five, Western Tanager ($r_s = 0.41$, $P = 0.03$) and Lark Sparrow ($r_s = 0.51$, $P = 0.001$), vagrancy to Massachusetts was significantly related to breeding abundance calculated at the continental scale. The correlation for Yellow-headed Blackbird also was positive ($r_s = 0.28$, $P = 0.09$).

At the regional scale (i.e. the eastern, central, and western thirds of North America), vagrancy in Massachusetts was significantly correlated with breeding abundance for Clay-colored Sparrow ($r_s = 0.48$, $P = 0.03$), Lark Sparrow ($r_s = 0.51$, $P = 0.007$), and Yellow-headed Blackbird ($r_s = 0.43$, $P = 0.02$). Vagrancy of the Lark Sparrow and Yellow-headed Blackbird was correlated with breeding abundance in the central part of North America, whereas vagrancy of Clay-colored Sparrow was related to breeding abundance in the western third of the continent.

At the scale of individual BBS strata, vagrancy in Massachusetts was correlated with population growth for all five species (Table 1). I compared the number of significant ($P < 0.1$) correlations (Table 1) with the number that would be expected due to chance, and found that for all five species, the observed number was greater than expected (Wilcoxon paired-sample test, $Z = -2.03$, $n = 5$, $P = 0.04$).

Visual inspection of the BBS maps (see Fig. 1) suggested that strata for which abundance was correlated with vagrancy in Massachusetts were clustered in space. To test if this clustering was more than would be expected by chance, I calculated combinations for each species using the formula:

$$\binom{n}{k} = \frac{n(n - 1) \ldots (n - k + 1)}{k!}, \quad (1)$$

where $n =$ the number of strata in which a species breeds and $k =$ the number of strata for which abundance was correlated with vagrancy in Massachusetts. Equation 1 represents the number of combinations of n objects, taken k at a time, that can be formed (Batschelet 1979). For example, Western Kingbirds breed in 34 strata. Using $\alpha = 0.1$, there were seven strata for which Western Kingbird abundance was correlated with vagrancy to Massachusetts (Table 1). I chose the stratum in which abundance was most highly correlated with vagrancy in Massachusetts and determined the probability that four of the remaining six correlated strata would be spatially contiguous with the first one (see Fig. 1). Using equation 1, I calculated this probability to be 0.013. For the other four species, these probabilities were 0.32 (Western Tanager), 0.30 (Clay-colored Sparrow), 0.007 (Lark Sparrow), and 0.47 (Yellow-headed Blackbird).

Discussion.—Analysis of the temporal pattern of vagrancy in Massachusetts, and its relation to temporal patterns of abundance in western North America, provide strong support for the idea that vagrancy is driven by population growth. Other factors (e.g. weather patterns) cannot be dismissed as being influential, but my results suggest a stronger role for population growth. All of the western passerines that have occurred in Massachusetts regularly enough to permit statistical analysis display evidence of a link between vagrancy and reproduction. Given the geographic scope of this analysis, it is remarkable that any pattern at all could be discerned. Thus, the consistency of positive associations across the five species suggests that further study of vagrancy will yield useful information on avian population dynamics. A continent-wide effort to measure both temporal and spatial variation in passerine reproduction is now underway (DeSante et al. 1996). Eventually, data from this program will permit a more direct analysis of the process described here.

Frequency distributions of distances dispersed by animals are most always leptokurtic (Kot et al. 1996). Recent mathematical models of the spread of growing populations (van den Bosch et al. 1992, Veit and Lewis 1996) have emphasized the importance of the
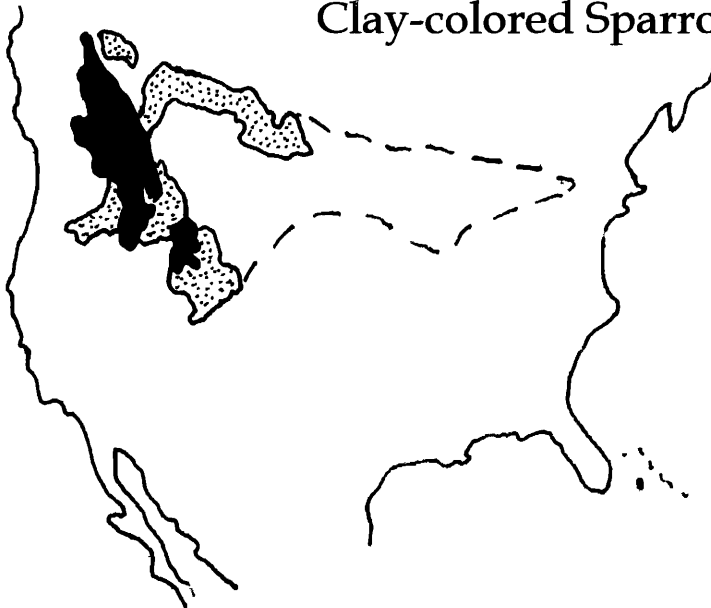
Western Kingbird
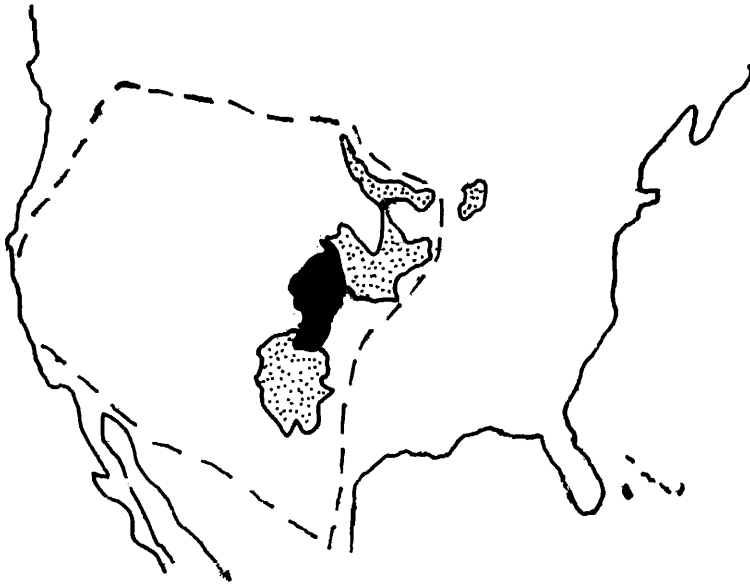
Clay-colored Sparrow

FIG. 1. Example of breeding distribution and abundance for two western North American passerines (Western Kingbird and Clay-colored Sparrow) that have occurred as vagrants in Massachusetts with a mean of at least five individuals per autumn from 1966 to 1988. Blackened regions represent BBS strata for which breeding abundance was correlated with number of vagrants in Massachusetts ($P < 0.05$), and stippled areas represent $P < 0.1$. Dashed lines delimit the breeding distribution of each species.

very long "tails" of these distributions and conclud-
ed that the rate of population spread is driven by the
small proportion of individuals that disperse much
farther than average. In populations of the five spe-
cies analyzed, some individuals traveled on the or-
der of thousands of km eastward each year. That this
eastward movement occurs in years of elevated re-
production is consistent with the mechanism of Veit
and Lewis (1996). This suggests that this model, or a
similar one, could be used to predict the likelihood
of colonization of newly created or revitalized patch-
es of habitat. Not every vagrant manages to breed;
indeed, most probably do not owing to the difficulty
of finding a mate and/or suitable habitat. However,
the mechanism inherent in the Veit and Lewis model
is that colonization is achieved by the inherent ten-
dency of growing populations to repeatedly generate
vagrants. Eventually, breeding occurs (e.g. Hengev-
eld 1989, Johnson 1994).

The strength of correlations between population
growth and vagrancy depended on the spatial scale
at which analyses were conducted. The strongest
correlations were obtained at the smallest spatial
scale, that of individual BBS strata, which are on the
order of hundreds of km in width. This is consistent
with Brown et al.'s (1995) finding of congruence of
abundance of passerines from BBS data on the scale
of hundreds of km (spatial autocorrelation dropping
off after about 500 km).

The strata within which breeding abundance was
correlated with vagrancy in Massachusetts tended to
be adjacent to one another. For the most part, va-
grancy in Massachusetts was correlated with breed-
ing abundance within that part of the breeding range
closest to Massachusetts. A dramatic exception was
the Clay-colored Sparrow. Vagrancy in Massachu-
setts was correlated with population growth in the
northwestern part of the breeding range, despite re-
cent range expansion by Clay-colored Sparrows to
the Lake Ontario region. This suggests that the ori-
gin of Massachusetts Clay-colored Sparrows is Brit-
ish Columbia, which is an area where population
growth is most evident. This possibility should not
be rejected out of hand. Brewer's Sparrows (*Spizella
breweri*) have appeared on the east coast (Veit and Pe-
tersen 1993), and Common Grackles (*Quiscalus quis-
cula*) have been recovered more than 2,600 km from
their site of banding (Moore and Dolbeer 1989). Sim-
ilarly, vagrancy of Yellow-headed Blackbirds in Mas-
sachusetts was most strongly correlated with popu-
lation growth along the north-central edge of the
breeding range, which is the same area where pop-
ulation growth of Yellow-headed Blackbirds has
been the most dramatic.

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Variation in the Number of Spermatozoa in Blue Tit and Great Tit Eggs

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In birds, fertilization takes place in the infundibulum at the top of the female reproductive tract. To reach this site, spermatozoa must travel from the hostile environment of the vagina, or from sperm-storage tubules located at the utero-vaginal junction, and on through the oviduct (Birkhead et al. 1993a). Only a minute fraction of the inseminated spermatozoa reach the site where eggs are fertilized, but the actual number varies considerably across species (Birkhead et al. 1994). By counting the number of spermatozoa in or penetrating the perivitelline layers of fresh eggs, it is possible to obtain an index of the number of spermatozoa present in the infundibulum at the time of fertilization (Birkhead and Fletcher 1994).

When released from the ovary, the ovum is covered by the inner perivitelline layer. Fertilization takes place 15 to 30 min after ovulation with one of several spermatozoa that penetrate the inner perivitelline layer (Bakst and Howarth 1977). Shortly after fertilization, the outer perivitelline layer is laid down on the ovum, trapping other spermatozoa present in the infundibulum (Wishart 1987). The number of holes in the inner perivitelline layer is correlated with the number of spermatozoa trapped on the outer layer (Birkhead and Fletcher 1994, Birkhead et al. 1994).

In this paper, we report on variation in the number of spermatozoa in eggs of two passerine species, the Blue Tit (Parus caeruleus) and the Great Tit (P. major), with a special focus on variation within and between clutches of individual females. The results are discussed in light of the mating system of these species.

Study areas and methods.—Eggs were collected in early May 1997 from two populations of Blue Tits and Great Tits that nested in boxes in southeastern Norway. One study site was located on the island of Jomfruland (58°52′N, 9°36′E) off the coast of Telemark County, where tit populations have been studied for several years (Krokene et al. 1998). On Jomfruland, we collected a maximum of three eggs from each clutch, which did not interrupt the normal nesting events. At the other study site, in Maridalen, Oslo (59°58′N, 10°47′E), we collected entire clutches of both species to study variation in total number of spermatozoa over the laying sequence. For the Blue Tit, the overall sample for analysis consisted of 107

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