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WHAT TO DO ABOUT THE NORTH AMERICAN INVASION BY THE COLLARED DOVE?

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Abstract.—The attention of American ornithologists is drawn to the North American invasion of a renowned European invader, the Collared Dove (*Streptopelia decaocto*). After the experience obtained in Europe, several aspects can now be studied in North America, (1) how the spread across the continent is progressing, (2) how the local populations build up, (3) whether, by using a recent model, the rate of spatial progression of the invasion wave can be predicted, (4) how much, where and when pheno-genetic differentiation is generated, and (5) how it affects the local fauna. Americans have a unique opportunity to study the invasion of one of the best-known invaders, on their own ground, on the basis of extensive experience from Europe.

¿QUÉ HACER SOBRE LA INVASIÓN DE *STREPTOPELIA DECAOCTO* EN NORTE AMÉRICA?

Sinopsis.—La atención de los ornitólogos norteamericanos se ha dirigido a la invasión de Norte América por parte de la paloma collarina (*Streptopelia decaocto*). Luego de la experiencia obtenida en Europa, varios aspectos poblacionales del ave pueden ser estudiadas en América: (1) cómo está progresando la expansión territorial del ave a través del continente, (2) cómo la población local ha ido creciendo, (3) si utilizando un modelo reciente, se puede predecir el progreso espacial de la invasión, (4) cuánta, dónde y cuándo se genera la diferenciación feno-genética y (5) cómo esto va a afectar a la fauna local. Los norteamericanos tienen una oportunidad única para estudiar la invasión de uno de los mejores colonizadores conocidos, teniendo como base la basta experiencia que ya hay con esta paloma en Europa.

This paper draws attention to several ways in which the invasion into North America of one of the best-known invaders from Europe (Fig. 1) can be studied. Utilizing this European experience, it explains which aspects of the invasion process can best be studied in a broad-scale survey of the continent. There are five main areas of interest: (1) the way the invasion progresses through space, (2) the local buildup of the newly settled populations, (3) the possibility of predicting the rate of invasion, (4) the pheno-genetic differentiation in the invaded area, and (5) the effect of this invader on native species. Curiously, the sequence of these areas of interest is counter to the interest of ecologists, although their tractability decreases.

HISTORY OF THE AMERICAN INVASION

The Collared Dove (*Streptopelia decaocto*) was introduced from the Netherlands into Nassau, New Providence, Bahamas by a pet breeder (Smith 1987). No more than 50 birds escaped in December 1974 and first nesting was observed the next summer in Nassau. In New Providence it quickly built up its population, and it spread to other islands. It is highly probable that the species spread from there to Florida, although the exact time and location cannot be reconstructed. They were observed

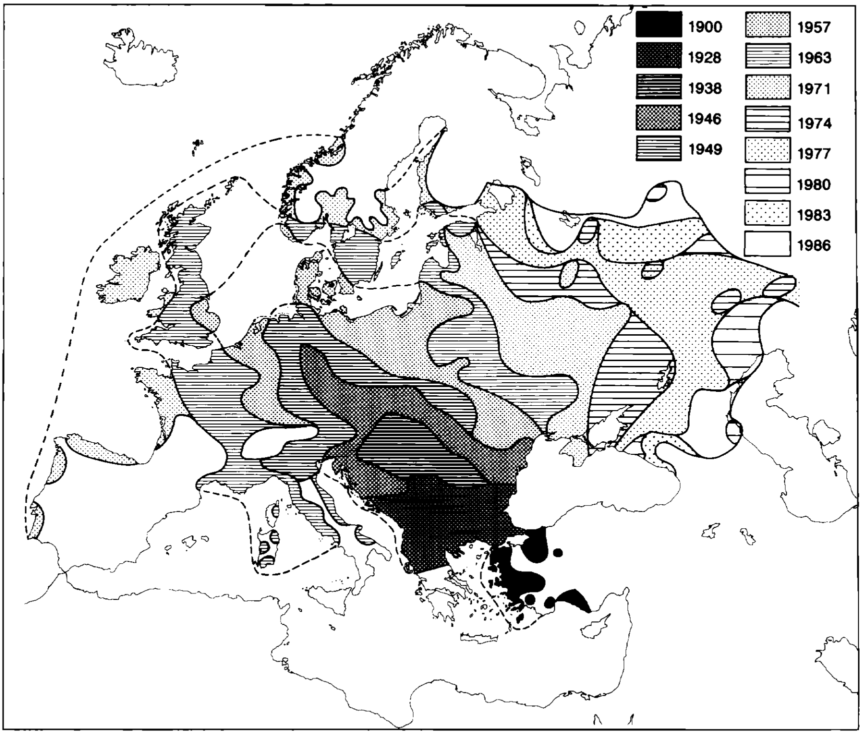

FIGURE 1. Expansion of the Collared Dove in Europe west of the Ural Mountains up to 1988 (combined after Hengeveld 1989 and Nowak 1989, 1991).

in the late 1970s in the Homestead area, where first breeding was observed in 1982, although other locations of first settlement in Florida seem likely. Since its initial settlement, it has spread quickly across Florida (Fig. 2) before penetrating the mainland (H. W. Kale, pers. comm.).

ECOLOGICAL EFFECTS

Traditionally, much attention is being given to effects invaders might have on the existing communities (e.g., Elton 1958). First, communities are classified as open or closed systems (cf. Pimm 1991), often done irrespective of the potential invader concerned. Independent criteria are often lacking, and if given, they are difficult to quantify. Community resistance would follow from a combined competition of native species. When the invader happens to break through this closed system, it would disrupt its balance, which would only gradually recover in a different form, possibly excluding one or more native species. Of course, such rigid systems will be rare, if they exist at all. Yet, assuming a looser structuring, much research on invasions is directed to ecological effects of invaders through taking over (parts of) niches already occupied.

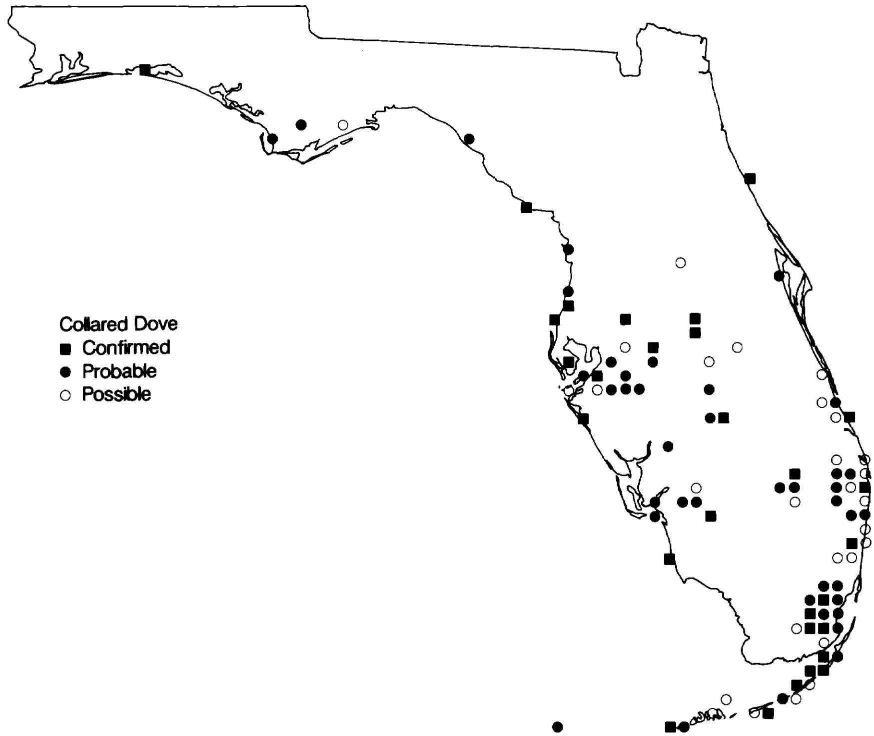

FIGURE 2. Distribution of the Collared Dove in Florida, September 1991.

For some species competition for food or nesting places has been claimed, but the Collared Dove seems not to have found obvious competitors in Europe. Only the Turtle Dove (*Streptopelia turtur*) has occasionally been mentioned, although it occurs in a different habitat. For the European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*) in North America, Dobson and May (1986) suggest that their success in America may partly derive from a smaller parasitic burden than in Europe. Neither parasitism, nor significant predation in the Collared Dove is known from Europe, although egg predation by crows has been mentioned (MacDonald 1984, Rucner 1952).

PHENO-GENETIC DIFFERENTIATION

Mayr (1951) suggested that invasions may be caused by a genetic change in peripheral parts of the species' geographical range. To my knowledge, no study exists about the genetics of peripheral populations of the Collared Dove, or of genetic differentiation from the main body of its Eurasian range. It would be interesting to see, therefore, if on the vast and ecologically varied sub-continent of North America such a differentiation could take place. In fact, it occurred within a relatively short time in the

European House Sparrow (e.g., Johnston and Selander 1971) in which skeletal dimensions differentiated, in association with environmental (temperature) conditions, but differently for the two sexes. Apart from this, temperature regulation, existence metabolism, reproduction and the daily energy budget also vary geographically (Blem 1973, Kendeigh 1976).

It is important to study differentiation right from the start of the initial Collared Dove invasion, as this gives insight into the rate at which it might develop.

THE PROCESS OF SPREAD

Broadly, one can conceive of two ways an invasion progresses, by a steadily rolling, laterally continuous wave, or by the coalescence of initial foci lying ahead of a spatially more coherent region of occurrence. In the first case, the contribution of individual organisms within the wave cannot be discerned, whereas in the second case the rate of wave progression largely, if not entirely, depends on it. The steady progression can best be described using deterministic models, and the invasion advancing through bridgeheads using stochastic ones. The latter models are of the reaction-diffusion type, in which the diffusion component stands for progression by random (Brownian) movements of the propagules. The reaction component stands for population growth immediately after the initial settlement of the propagules. Of these two types, the first, deterministic one is fed by propagules dispersing only a very short distance from their parent. The second, stochastic way of progression is fed by occasional long-distance dispersers; the subsequent process of population coalescence is again fed by short-distance dispersal.

Apart from reflecting the two types of process exactly, these types can also result artificially from choosing either a coarse or a fine spatial sampling resolution, respectively (cf. Hengeveld 1989). The finer one looks, the better one sees the movements of the individual organisms; what seems to be a continuous wave may in fact be a system of isolated bridgeheads. A criterion for discriminating the two types explicitly without getting involved with sampling problems is the shape of the wave front. If it mainly reflects population growth after settling, then dispersal hardly plays an independent role; the wave progresses deterministically. If, however, the front reflects the shape of the distance distribution of the new breeders relative to their parents, then the wave progression is stochastic.

It seems that in Europe, wave progression was stochastic. Plotting the distances between young breeding birds relative to their parents' nest, we obtain a leptokurtic distribution (Fig. 3). This distribution is probably composed of two stochastic processes, a Gaussian spread of individuals around their parents' nest, and an exponential trapping of dispersing birds by the environment away from the nest (Broadbent and Kendall 1953). The result is a modified Bessel function, shaped depending on both the intensities of Gaussian movement and the trapping rate. Figure 4 depicts actual bridgeheads beyond the more closed front.

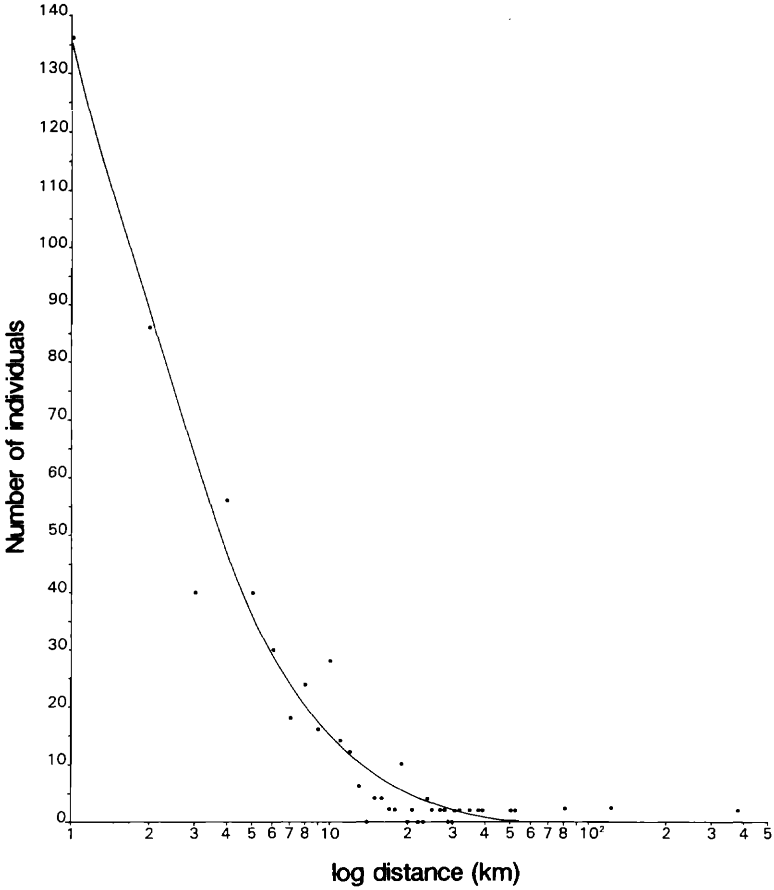

FIGURE 3. Frequency distribution of dispersal distances.

POPULATION BUILD UP

Biologically no less interesting is local population growth. Figure 5 shows that for the Netherlands and for Great Britain it was exponential for a considerable time; the exact period of local population saturation is not known, nor are the factors causing saturation. As the British data include both the number of breeding birds and that of the localities, we can calculate the spatial saturation rate (Table 1).

It would be extremely interesting to follow the buildup of the population of the Collared Dove at several localities in North America to compare their growth statistics. These statistics include the local net-rate of reproduction, R_0, the asymptotic value K of the logistic, as well as the time and rate at which K is reached under the widely different biotic and abiotic conditions found in North America.

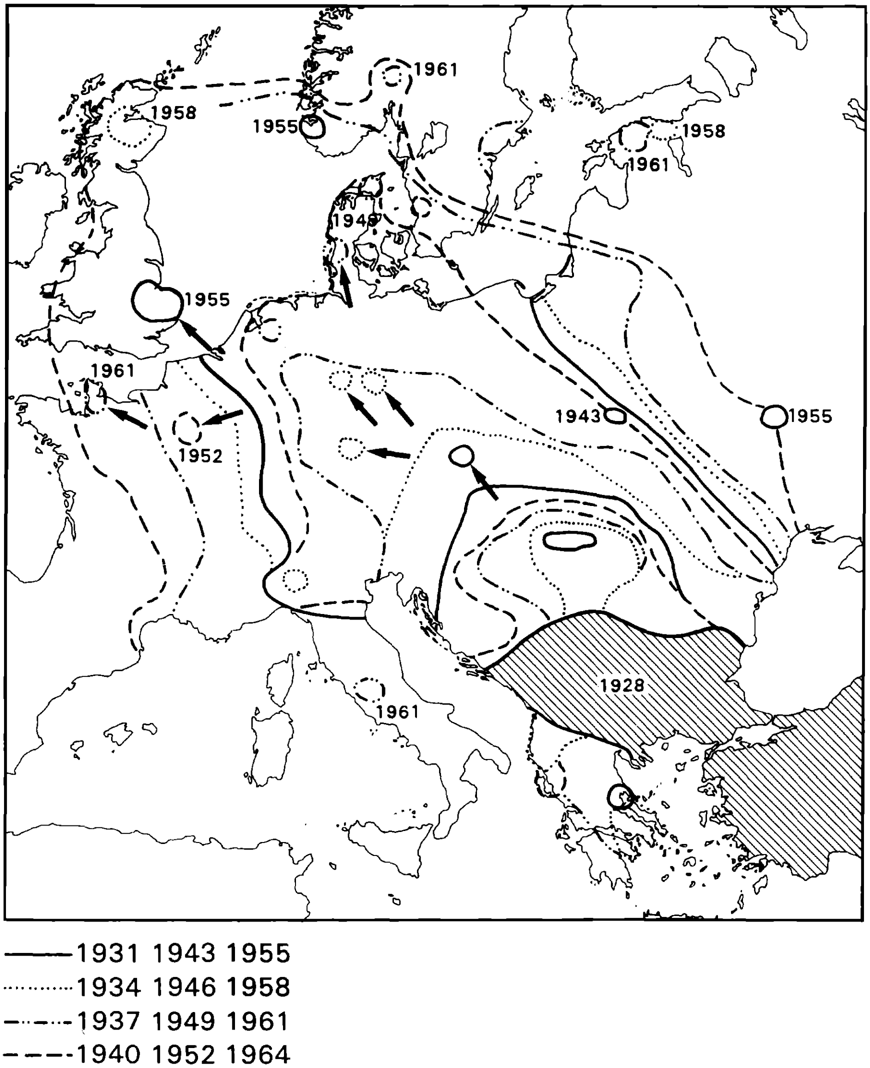

FIGURE 4. Expansion of the Collared Dove in Europe emphasizing far outlying bridgeheads (after Nowak 1977).

PREDICTING THE INVASION RATE

The estimation of expected invasion rates should preferably not use data from the wave itself to prevent circular reasoning (Hengeveld and Van den Bosch 1991, Van den Bosch et al. 1992). Therefore, we did not use statistics that could have been obtained from Figures 3–5. Instead, we used banding data from inside the geographical range away from the

TABLE 1. Increase in the number of breeding Collard Doves, the number of locations occupied, and the spatial saturation rate as the ratio of these two parameters (according to British data in Hudson 1965).

	Individuals			Locations			
Year	n	log n	$\frac{\log(t+1)_n}{\log(t)_n}$	l	log l	$\frac{\log(t+1)_l}{\log(t)_l}$	$\frac{\log n}{\log l}$
1955	4	0.60	—	1	0.00	—	—
1956	16	1.20	2	2	0.30	—	4.00
1957	45	1.65	1.37	6	0.78	2.58	2.12
1958	100	2.00	1.21	15	1.18	1.51	1.69
1959	205	2.31	1.16	29	1.46	1.24	1.58
1960	675	2.83	1.22	58	1.76	1.20	1.61
1961	1900	3.28	1.16	117	2.07	1.17	1.58
1962	4650	3.67	1.12	204	2.31	1.12	1.59
1963	10,200	4.01	1.09	342	2.53	1.09	1.58
1964	18,855	4.28	1.07	501	2.70	1.07	1.59
1970	95,000–158,000	4.98–5.20	1.19	—	—	—	—
1972	190,000–253,000	5.28–5.40	1.05	—	—	—	—

invasion front for calculating the mean, the variance and the kurtosis of the distance distribution (Fig. 6). Also, for calculating the net-reproductive rate, we used literature data on survival and fertility per age class from established populations within the range assembled in a Leslie matrix (Table 2). The age interval does not refer to subsequent years, but to periods within the year, because this dove reproduces several times per year: in Europe roughly from March to November, occasionally even during the winter months. Breeding should therefore be monitored throughout the year. When this procedure is followed for banded birds, one also gets information on the time within the year the invasion progresses, i.e., whether it is continuous throughout the year or whether it relates to migratory movements confined to particular months. So far, it is not clear which process is occurring.

Utilizing estimates of the rates of net-reproduction and of dispersion, the expected wave velocity can be calculated using formulas for net-reproductive rate, mean age at first breeding, dispersion rate, and the expected wave velocity. The value of this last statistic, C_{exp}, can be compared with that of the observed velocity, C_{obs}, obtained from the mapped range expansion. The regression of the square root of the area occupied by the invader against time gives the estimate of C_{obs} required (see Hengeveld and Van den Bosch (1991) for the exact equations and their application).

SENSITIVITY TO ECOLOGICAL VARIATION

These parameter values will vary due to environmental variation, and so will the resulting expected wave velocity, C_{exp}, for North America. In fact, the Collared Dove will eventually reach its North American range

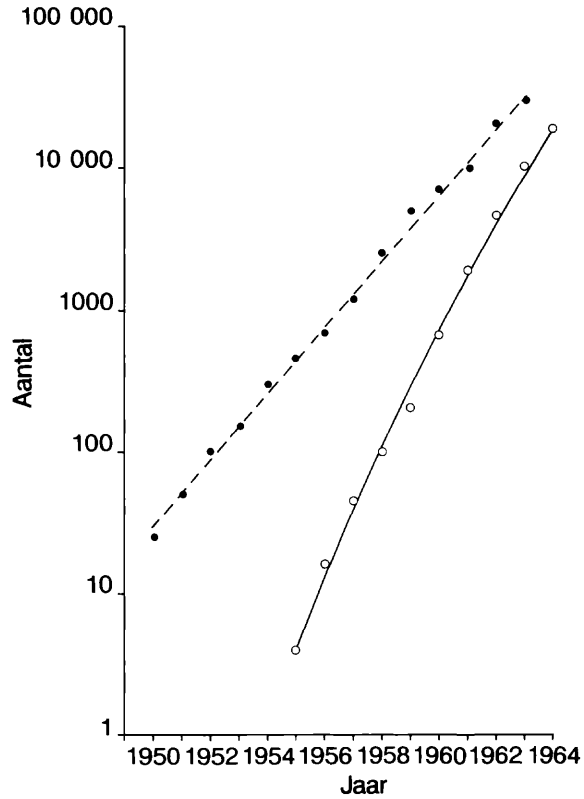

FIGURE 5. Growth of the total population of the Collared Dove in Britain and Ireland after its first settlement in 1955 (open circles) (after Hudson 1965, 1972) and in the Netherlands (dots) (after Leys 1967).

limits at some point, which necessitates that estimates of these values for different conditions be included in the calculations of regional wave velocities.

Part of the environmental variation affects the reproduction component of the settling populations and another part affects spatial spread, the latter also being partly dependent on reproduction. Reproductive capacity depends on the local reproductive rate and this rate, in turn, depends on the survival rate of the population as well as on the fertility rate per age class. Both parameters are under environmental control. The formulas used include the proportion of females in the population, which in some species is affected by environmental variability, but not in others. The spreading component partly depends, as does the newly settled population, on reproductive rate of the individuals and partly on their mobility, as well as on the trapping by the environment. All parameters depend on environmental factors, mobility through the activity of the individuals

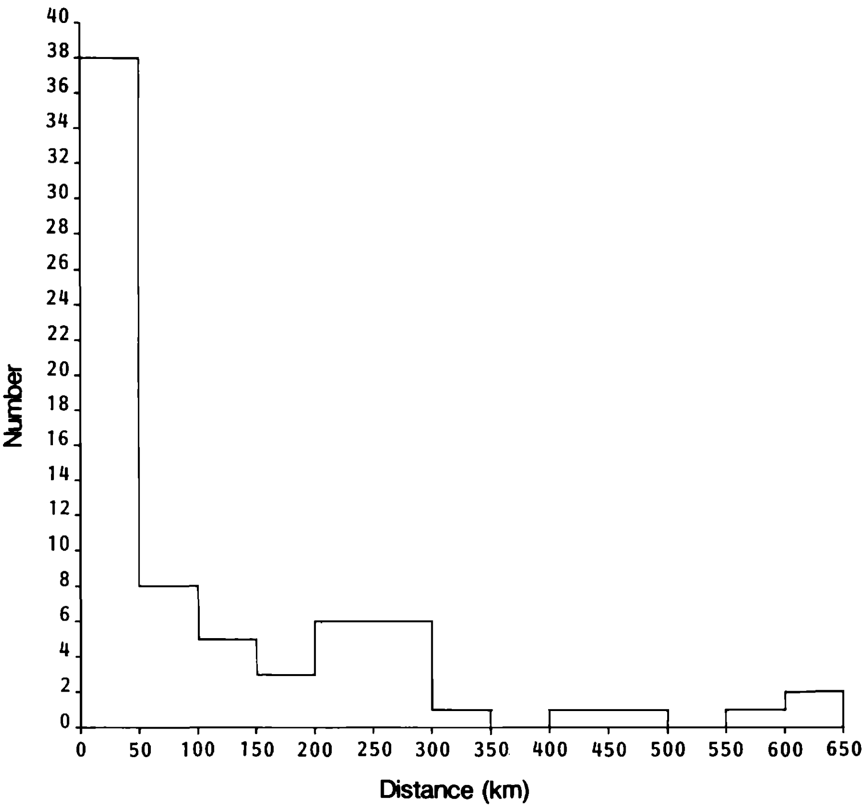

FIGURE 6. Frequency distribution of dispersal distances of the Collared Dove according to banding records (data obtained from Euring data bank, Heteren, Netherlands).

and the trapping rate on the frequency and patterning of favorable and unfavorable conditions and habitats. Thus, a slight change in survival rate of the Collared Dove, involving greater mortality in the younger age classes (Table 3), decreases net-reproductive rate R_0 from 1.33 to 0.74 and, hence, the expected wave velocity, C_{exp}, from 56.3 to 32.5 km/yr (Hengeveld, 1992).

Close, yet broad-scale observations are needed to explain and predict the regional vicissitudes and fate of the invasion of the Collared Dove in North America.

DISCUSSION

The invasion of the Collared Dove into North America gives a unique opportunity to study several aspects common to all invasions. One advantage of studying this species in particular is that its invasion into Europe is exceptionally well documented (cf. Fisher 1953; Glutz von Blotzheim and Bauer 1980; Gorski 1989; Hengeveld 1988, 1989; Hen-

TABLE 2. Calculation of the net-rate of reproduction, R_0, of the Collard Dove from life-history data on survival rate, $L(a_i)$, and fertility m (a_i) per age class.[1]

Age interval	Median age	Survival	Fertility	Reproduction
0–0.5	0.25	0.86	0	0
0.5–1	0.75	0.52	0.313	0.163
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
4–4.5	4.25	0.001	3.125	0.031

[1] $\Sigma L(a_i) \cdot m(a_i) = R_0 = 1.33$.

geveld and Van den Bosch 1991; Hofstetter 1960; Hudson 1965, 1972; Nowak 1965; Stresemann and Nowak 1958). In addition, it is easy to sight and its voice carries and is characteristic. Moreover, for several decades, amateur birders in North America have been well organized and are already doing a good job on their breeding bird counts (Robbins et al. 1986) and their Christmas counts (Root 1988). Finally, the invasion started in one corner of North America (Smith 1987) (Fig. 2), and will fan out spectacularly across an essentially square continent. Latitudinal and longitudinal effects can therefore ideally be distinguished.

The projects to be formulated would center around the various topics as recognized here. The effects the Collared Dove can have on native ecosystems or species can be partly identified from the usual observations done routinely in the breeding bird survey. For another part, it may be necessary to do special observations on possible shifts in food choice of several of the species with the largest ecological overlap, on predation, and external and internal parasitism and disease.

The pheno-genetic differentiation could follow the exemplary studies by Johnston and Selander (1971), Kendeigh (1976) and Blem (1973) on the House Sparrow. It would be an essential addition to their studies, however, to include the time component by following the possible differentiation from the first settling onwards for a number of locations. Also, toes and legs should be observed, as they can be badly affected by low winter temperatures.

The gradual extension of the new range can be followed at three levels of spatial resolution: a coarse one for identifying the annual progress of the invasion wave without reference to individual birds, an intermediate one for the study of spatial saturation, and a fine one based on their individual identity. To the latter end, the birds should, ideally, be banded at their nests as young birds. Then, similar to what Fisher (1953) did in Europe, maps can be constructed giving the locations of these individual breeding birds and distances measured between their own nesting sites and their parents'; the distance distributions can vary across the continent. Thus, although taking the greatest effort, the highest resolution is much preferred to the intermediate and coarse ones.

Population growth after settlement is obviously of great interest in two respects. In different parts of the continent, net-reproductive rate and the

TABLE 3. Calculation of the net-rate of reproduction, R_0, of the Collared Dove with an artificially changed survival rate.

a_i	$L(a_i)$	% change	$L(a_i)$50%
0.25	0.86	—	0.86
0.75	0.52	0.60	0.43
1.25	0.31	0.60	0.22
1.75	0.23	0.74	0.11
2.25	0.13	0.57	0.05
2.75	0.07	0.54	0.03
3.25	0.04	0.57	0.01
3.75	0.02	0.50	0.005
4.25	0.001	0.50	0.002

asymptotic value, K, of the logistic equation can vary due to differences in ecological conditions. This gives a unique opportunity to investigate the mechanisms causing population growth from scratch. As many factors affect the rates of survival and fertility, careful analysis should be planned in each case; this analysis can also include experimental work along with field observations. Particularly for these studies, it seems necessary to design a geographical pattern of sampling areas in advance, at least including the main biomes, but preferably some finer-scale units as well.

Having information on dispersal and population growth both at the invasion front and in the already established parts of the range allows predictions to be made as to the future course of the invasion. These predictions, utilizing different sets of data, can then be compared, and the possible causal mechanisms evaluated.

The whole scheme obviously requires an enormous amount of work. It will therefore be practical to make a priority list. The one I would suggest is to band young birds at their nests and administer the data as accurately as possible throughout North America. Second, estimates of the components of regional population growth are essential in several respects, giving highly rewarding results. The third point on the list could be the identification of first bridgeheads beyond the wave front and the subsequent filling in of the area between by second-order settlements. After this identification, a temporally coarse-scale monitoring of parasitism can give invaluable insight into the compositional buildup of this fauna over time, together with an estimate of its possible burden to the Collared Dove. However important the remaining aspects are ecologically, the pheno-genetic differentiation and ecosystem effects of this invasion, these aspects will almost certainly require too much effort for broad-scale monitoring to be successful. They should, to my mind, be left to local groups of specialists.

CONCLUSIONS

The invasion of the Collared Dove into North America offers an ideal and unique opportunity to study this invasion once more after its success in Europe (Hengeveld 1988, 1989; Stresemann and Nowak 1958). Using all the European experience and utilizing a well-running organization for monitoring birds at a broad, continental scale in North America, efficient and directed observations can now be made. From its success in Florida, we can suspect a rapid invasion of this species into the rest of North America, justifying special projects to be set up rapidly. The great insights gained from such studies in Europe fully warrant extra attention in America.

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