

Effects of asexual reproduction on the neighborhood area of cyclical parthenogens^{*}

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Key words: genetic structure, effective population size, neighborhood area, monogonont rotifers, cyclical parthenogens, parthenogenesis, gene flow

Abstract

The habitat occupied by a subpopulation and within which there is random mating is known as its 'neighborhood area'. Neighborhood area is dependent on dispersal rates and organisms with low rates of dispersal are expected to have small neighborhood areas. In the absence of evolutionary forces, neighborhood areas under sexual reproduction will be constant in size as long as dispersal patterns do not change. This scenario differs when reproduction is by cyclical parthenogenesis since recombination and dispersal may occur in different generations. In general, dispersal distances increase with the number of parthenogenetic generations. We show that cyclical parthenogenesis increases neighborhood area which, concomitantly, decreases the potential for genetic subdivision. It is noteworthy, however, that the increase in neighborhood area is a decreasing function of the number of parthenogenetic generations.

This mechanism may have important implications for the population structure of planktonic rotifers living in a horizontally undifferentiated habitat. In such habitats organisms are effectively unrestricted in their lateral movements. Because rotifers typically have low dispersal rates spatial genetic discontinuities may develop that divide the population into genetically distinct subpopulations. Countering this tendency is the increased neighborhood area produced by dispersal during the parthenogenetic phase. Thus cyclical parthenogenesis in organisms like rotifers may have important and previously unreported effects on the population's genetic structure.

Introduction

From a human perspective, planktonic rotifers are small and, like other organisms whose rates of movement are measured in mm min^{-1} , have limited abilities to disperse. Again from a human perspective, many of the lakes occupied by rotifers are quite large. Taken together these observations suggest that gene flow is not likely to occur between widely-separated individuals in the same lake.

Patterns of gene flow are of great interest to the population biologist because they are a major factor in determining population structure. When a population is spread over a large area relative to its dispersal ability, the potential exists for division of the popu-

lation into subpopulations that may undergo independent evolution. This process acts to increase genetic diversity among subpopulations. However, as populations become more and more subdivided there is an increased potential for loss of genetic variation within subpopulations by random genetic drift. Thus in many subdivided populations there is low variation within and high variation between subpopulations.

When considering the effects of population structure on potential for genetic change, size of the population is best measured not by the actual number of individuals, but rather by the effective population size. Effective population size is the theoretical number of individuals within a population having an equal probability of randomly mating and contributing alleles to the next generation. Because of factors such as temporal variation in numbers, unequal numbers of males and females, and variation in number of offspring per

^{*} This paper is dedicated to Professor K. Hirayama on the occasion of his retirement.

individual, the effective population size is often considerably smaller than the actual number of individuals in the population.

The geographical area occupied by the randomly-mating individuals in a given subpopulation is known as its ‘neighborhood area’. In a continuously distributed population, such as planktonic rotifers in a lake, the habitat may become divided into neighborhood areas reflecting the dispersal abilities of the individuals in the population. If these neighborhood areas are small relative to the total habitat size, subpopulations may become locally differentiated. Large neighborhood areas promote patterns of uniform genetic diversity and retard independent evolution in different geographical areas.

In this paper we deal with the relationship between reproductive mode and neighborhood area in a continuously-distributed population. In particular, we will show that the asexual phase of reproduction of cyclical parthenogens has the potential to greatly expand the size of neighborhood areas relative to their size for comparable organisms having obligate sexual reproduction. Parthenogenesis may therefore have an important role in determining genetic structure.

Wright’s neighborhood model

Dispersal and gene flow, frequently referred to as ‘migration’ in the literature of population genetics, are fundamental processes that potentially have important effects on allele frequencies in populations. For populations having patchy distributions in spatially heterogeneous environments, these effects are usually modeled by assuming partial reproductive isolation between the patches. The classical ‘island model’ of gene flow is one example of such an analysis. By contrast, a major complication arises when the population has a more or less continuous distribution without sharp boundaries. The relatively unstructured open water habitat occupied by plankton falls into this category. For planktonic rotifers, the distance traveled by an average individual between its birth and death is likely to be quite small.

Wright’s (1946, 1969) neighborhood model is appropriate for a continuously distributed population in which mating is random and there is a Poisson distribution of offspring numbers among parents. Let us assume that the parental individuals in a subpopulation are born at a central point, and then disperse in random directions. The offspring of these parents will have

birthplaces that vary in distance from the central point by σ , the standard deviation of the individual dispersal distances moved by all members of the subpopulation. Moreover, a circle of radius 2σ around the central point will contain the birthplaces of 86.5% of the offspring. The area of this circle was termed the ‘neighborhood area’ (NA) by Wright, and is equal to $4\pi\sigma^2$.

The neighborhood area is the spatial unit containing the effective number of individuals, N_e , in the subpopulation. That is, $N_e = 4\pi\sigma^2d$, where d is the genetically effective density (Wright, 1969). N_e is often referred to as the ‘neighborhood size’ when used in this context.

The variance term in the above equation, σ^2 , has a single source in Wright’s model, namely the movements of sexual individuals. In cyclical parthenogens this term includes the movements of both sexual and parthenogenetic individuals. Since it is reasonable to assume that the variance contributions from sexual individuals will be the same in both life history types, the remainder of this paper will focus on contributions derived from the dispersal of parthenogenetic individuals. For simplicity, we will assume that all individuals move a fixed distance in each generation which produces a variance derived exclusively from differences in directions of movement, and thus net distance moved, as a function of the number of parthenogenetic generations.

Dispersal distances in rotifers

Our purpose in this paper is to explore the consequences of cyclical parthenogenesis on neighborhood area rather than to obtain measures of neighborhood area in rotifer populations. However, for purposes of clarity, we will illustrate the conceptual operation of this model using data obtained from laboratory studies of monogonont rotifers. The first measure required is the linear distance moved between birth and reproduction. Fortunately, rotifer swimming behavior has been studied extensively, particularly at the Université Lyon by Clément and his colleagues. Rotifers swim in a helicoidal pattern and make frequent turns at varying angles. Coulon et al. (1983) describe an automatic tracking system for measuring rotifer swimming movements under a microscope. This system follows a single individual and records x and y coordinates every 1/12 sec. These coordinates are input to a computer and used to analyze movement rates, turning angles, and ‘distance as the crow flies’ (the net dispersal distance) over time. Using this system, Luciani et al.

(1983) determined an average velocity for young *Brachionus plicatilis* of approximately 0.6 mm s^{-1} , and a net rate of approximately of about 3 mm min^{-1} . Dispersal rates show substantial variation in both uniform culture media (Luciani et al., 1983) and in response to variables such as nutritional state of the female and food concentration (Charoy, 1995). For the purposes of our paper, the net dispersal rate of 3 mm min^{-1} will be used to obtain a crude estimate of dispersal distance. Note that this measure can be extrapolated to determine the distance of dispersal in a single generation, but it does not provide information on location because different individuals starting at the same point will move in different directions. This complication will be considered in the next section. We emphasize that this illustration only applies to one aspect of dispersal – the net distance individuals swim in a given period. Our model does not take into account dispersal by wind, water currents, or movements of resting eggs.

Snell & Childress (1987) found that males of *B. plicatilis* have about 30 sperm at birth, release 2.3 ± 0.36 sperm in a single copulation, mate frequently under their experimental conditions, and exhaust their sperm supply by the time they are 1 day old. In females of many loricate rotifers, fertilization must occur in the first few hours after birth. Snell & Childress (1987) found that fertility declined after an age of 4 hours for *B. plicatilis* and mictic females became infertile by the time they were 1 day old. Buchner et al. (1967) determined that mictic females of *Asplanchna sieboldi* had declining fertility after an age of 45 minutes and could not be fertilized after an age of 4 hours. Since both male and mictic female rotifers rapidly decline in fertility, most sexual reproduction occurs between young individuals who are born in proximity of each other. For example, during a 3-hour period at the net dispersal rate determined by Luciani et al. (1983), a rotifer moves approximately 0.5 m. This suggests, ignoring possible differences in net swimming rates between males and females, that the members of a mating pair are likely to have been born within a distance of about one meter of each other.

Standard deviation of dispersal distances

Dispersal of successive parthenogenetic generations was modeled as an unrestricted random walk in three dimensions. At each step, an individual moves in a straight line in a randomly-selected direction for r units of distance. The individual's net displacement

from its point of origin after a sequence of steps is $\sqrt{x^2 + y^2 + z^2}$ where (x, y, z) are the Cartesian coordinates of the individual's current position. The mathematical theory of random walks is well developed (e.g. see Barber & Ninham, 1970), but we chose to obtain distributions of dispersal distances using computer simulation. The results, presented for each choice of r , summarize 5000 simulations of a random walk consisting of 20 steps (generations). Each of the simulations is equivalent to the pathway of a single individual and its descendants (one per generation).

If sexual reproduction were to occur every generation, barring changes in the dispersal rates, neighborhood area would remain constant. When parthenogenesis intervenes between successive generations of bisexual reproduction, each parthenogenetic generation has its own period of dispersal. The net result is an additive process of increased distance from the point of origin of the last sexual generation.

We have used a 2-dimensional projection of the 3-dimensional dispersal distances obtained from our simulation model to calculate neighborhood area. Neighborhood area was analyzed for three values of r . The lowest, $r=0.541 \text{ m}$, would be equivalent to the distance moved in a time period, T , of 3 h. Values of r equivalent to $T=30 \text{ h}$ ($r=5.41 \text{ m}$) and $T=60 \text{ h}$ ($r=10.82$) were also used. Note that 30 h is a reasonable estimate of the generation time of many rotifers under optimal conditions, whereas a 60-h generation time is indicative of a population that is increasing much more slowly.

Results from the random walk model are presented in Figure 1 for the $T=30 \text{ h}$ population. While direction of dispersal varies randomly, each individual in the subpopulation moves a fixed distance in every generation. Thus, after one generation of dispersal at the $T=30$ rate, all 5000 individuals are located on the circumference of a circle whose radius is 5.4 m. In the second generation each individual again moves 5.4 m, but because of angular differences in their dispersal direction some individuals move closer while others move farther from the point of origin. After 2 generations of dispersal, the average individual is located $7.1 \pm 2.72 \text{ m}$ from the point of origin. This distance increases with further generations of dispersal until in generation 20 the average individual is located $22.2 \pm 9.58 \text{ m}$ from the origin. Additional data are presented in Table 1. Comparable determinations for the $T=60 \text{ h}$ population show dispersal distances of $14.3 \pm 5.51 \text{ m}$ in generation 2, and $44.4 \pm 18.93 \text{ m}$ in generation 20.

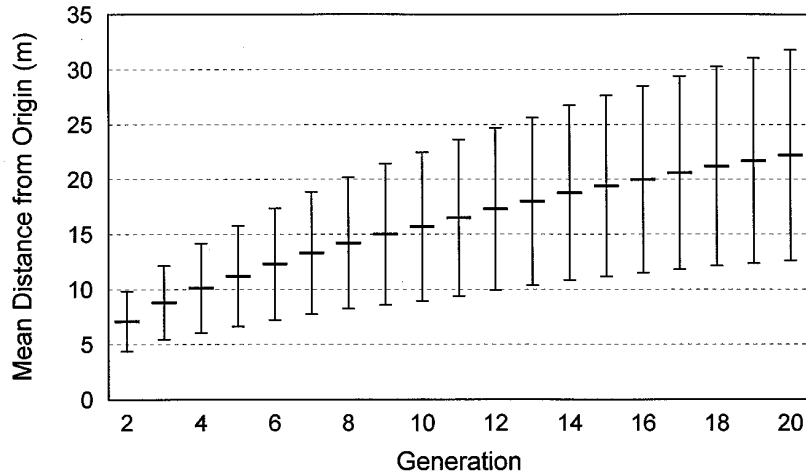


Figure 1. Mean ($\pm\sigma$) dispersal distances (m) for the $T=30$ h population after a varying number of generations of parthenogenesis.

Table 1. Mean dispersal distances (D , in meters), standard deviations (σ), and neighborhood areas (NA in m^2) for 20 generations (G) of three populations differing in generation time (T in hours).

G	$T=3$			$T=30$			$T=60$		
	D	σ	NA	D	σ	NA	D	σ	NA
1	0.5	–	–	5.4	–	–	10.8	–	–
2	0.7	0.28	1	7.1	2.72	93	14.3	5.51	381
4	1.0	0.40	2	10.1	4.06	208	20.0	8.05	814
6	1.2	0.50	3	12.3	5.08	324	24.6	10.34	1344
8	1.4	0.60	5	14.2	5.97	448	28.4	12.07	1831
10	1.6	0.68	6	15.7	6.76	574	31.6	13.56	2312
12	1.7	0.74	7	17.3	7.39	685	34.5	14.94	2804
14	1.9	0.81	8	18.8	7.96	796	37.3	16.19	3293
16	2.0	0.87	10	20.0	8.51	909	39.8	17.18	3708
18	2.1	0.93	11	21.2	9.06	1031	42.2	18.17	4149
20	2.2	0.97	12	22.2	9.59	1155	44.4	18.93	4505

Neighborhood area is based on the variation in movements among individuals. Distributions of net dispersal distances are presented in Figure 2 for generations 3, 5, 10 and 20 of the $T=30$ h population. Note that the distribution is strongly leptokurtic in generation 3 but in later generations becomes more symmetrical. The $T=60$ simulation has the highest rate of dispersal, each individual moving 10.8 m per generation. Because the curve of the dispersal distances becomes broader in each generation, the $T=60$ population initially has an increase in distance from the origin of about 3.5 m per generation. This value rapidly decreases to about 1 m per generation by generation 20 (Table 1).

Neighborhood areas for each of the three dispersal rates are shown in Figure 3. Not surprisingly, dispersal distance per generation is the major determinant of neighborhood area. Increasing dispersal distance by a factor of 10, from 0.54 m per generation to 5.4 m per generation, increases neighborhood area by a factor of about 100.

The number of parthenogenetic generations also contributes significantly to neighborhood area. For a given dispersal rate, increasing the number of generations by a factor of 10, e.g. from 2 to 20, increases neighborhood area by a factor of about 12. Note, however, that the increase is not uniform across generations. Figure 4 shows how neighborhood area increases with generation number. The incremental increase

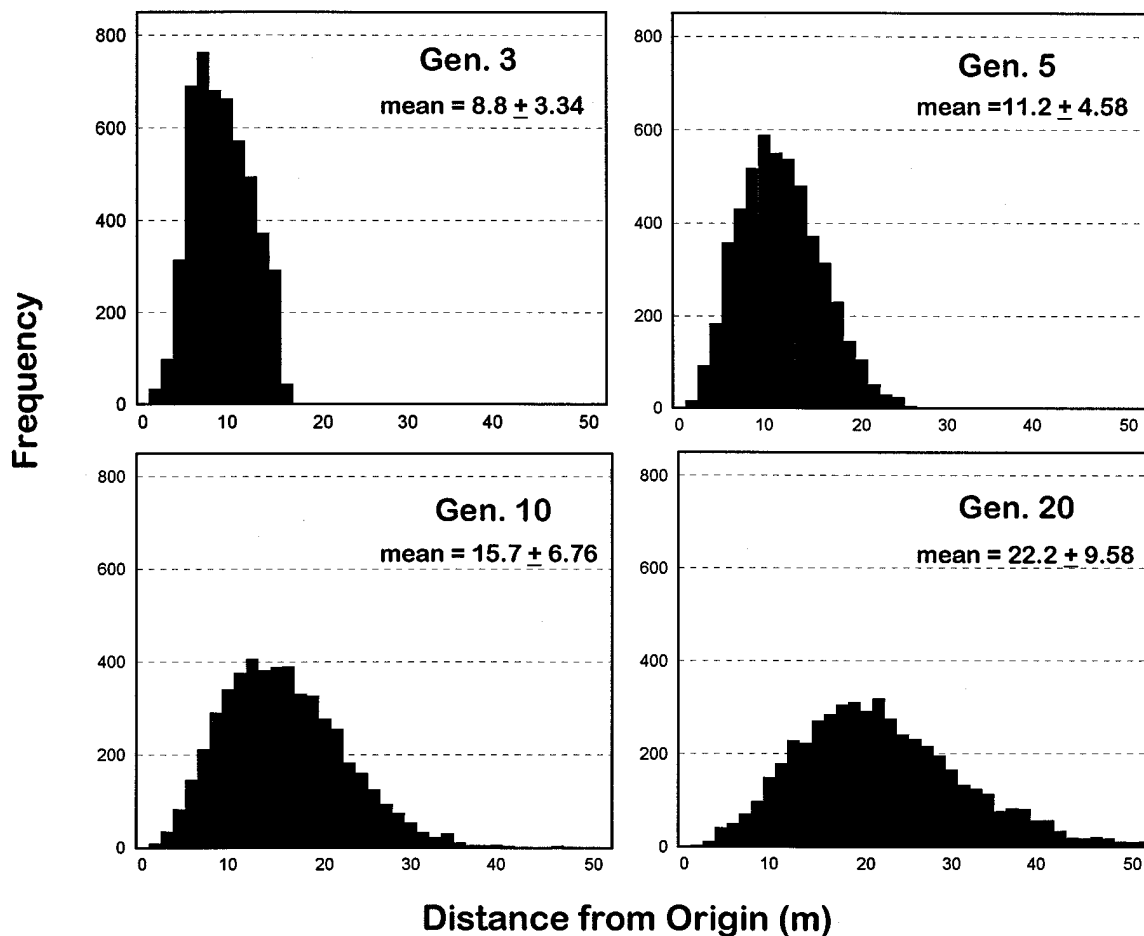


Figure 2. Frequency distribution of net dispersal distances (m) for the $T=30$ h population in generations 3, 5, 10, and 20.

per generation is initially large (>40% until generation 5), but declines to about 5% by generation 15 and changes very slowly thereafter. The shape of this curve has important implications. Relatively few generations of parthenogenesis may be needed to acquire large neighborhood areas. This means that genetic isolation by geographic distance is significantly decreased by asexual reproduction.

Discussion and conclusions

The asexual phase of cyclical parthenogenesis is usually considered as an adaptation producing rapid population growth which ultimately results in a greater number of mictic females and an increased number of sexual offspring. The ameiotic parthenogenesis of rotifers,

for example, increases the number of amictic females so that when environmental cues elicit sexual reproduction, large numbers of mictic females and sexual resting eggs are formed. Accompanying the increase in number of amictic females is an increase in population density.

The effect of parthenogenesis described in this paper is independent of population growth. We assume that as neighborhood area increases, the density of individuals remains constant and the population has both a stable and stationary age distribution. Under this model and in the absence of recombination and stochastic effects, the distribution of allele frequencies will not change as neighborhood area increases. Consequently, samples taken from large neighborhood areas are expected to have the same genetic composition as those from small neighborhood areas. Note that this model

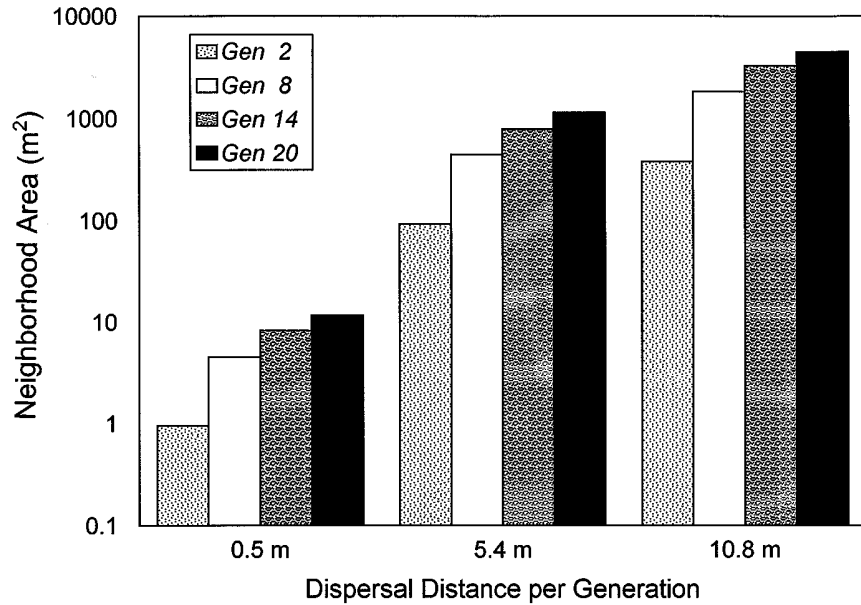


Figure 3. Neighborhood areas (m^2) in generations 1, 3, 5, 10 and 20 for the $T=3$ h, 30 h, and 60 h subpopulations.

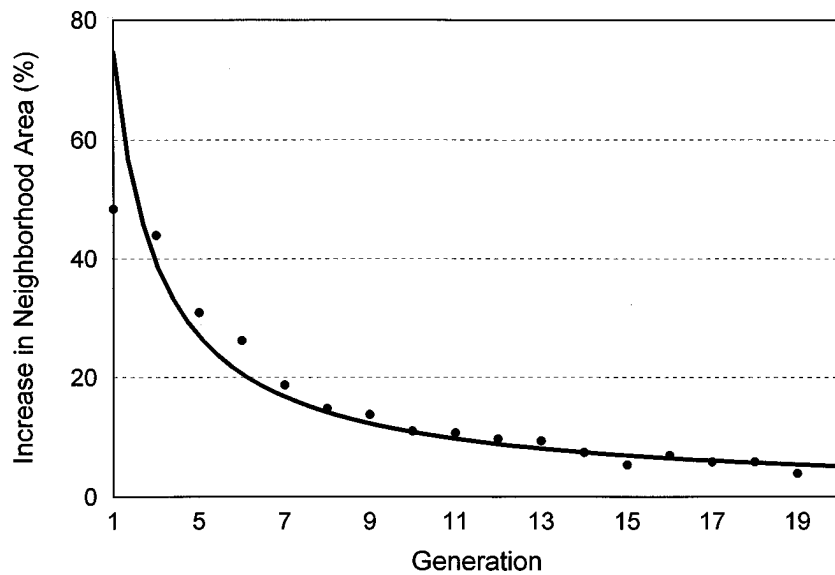


Figure 4. Percentage increase in neighborhood area of the $T=60$ subpopulation as a function of the number of parthenogenetic generations since last occurrence of sexual reproduction. The equation of the regression curve is $\log_e Y = 4.313 - 0.928 \log_e X$.

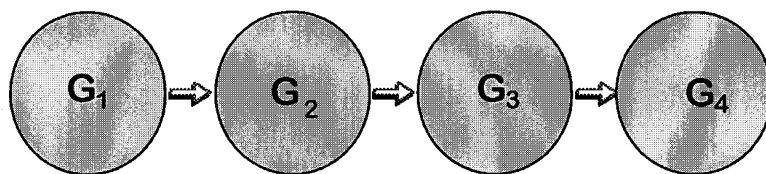
also assumes the absence of natural selection and other evolutionary forces during parthenogenesis.

In a less hypothetical situation, dispersal rates are likely to vary not only among individuals and genotypes within species, but also from one species to another, from one habitat to another, and from one set of conditions to another within the same habitat.

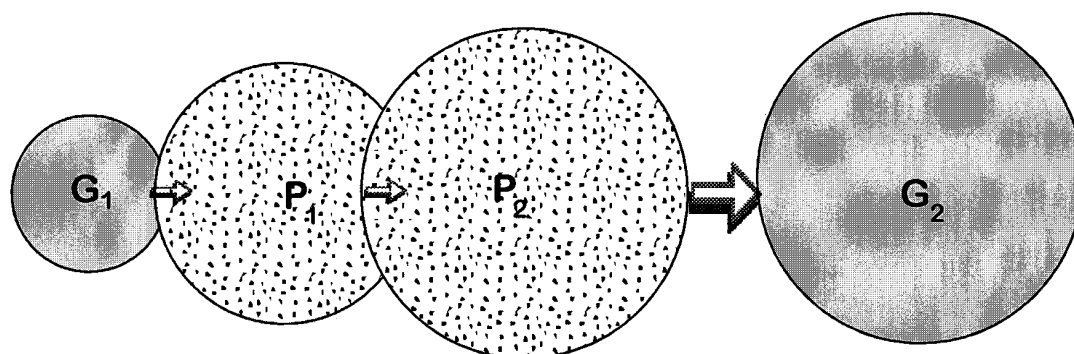
However, the central point of this paper is qualitative and variation in our assumed dispersal parameters is expected to scale the results up or down rather than to change the conclusions.

Neighborhood area in cyclical parthenogens is determined by two factors: (1) variation in the net dispersal distance moved by individuals and, (2) by the

Effect of Reproductive Mode on Neighborhood Area



Sexual Reproduction



Cyclical Parthenogenesis

Figure 5. Schematic comparison of neighborhood areas of sexually-reproducing organisms and cyclical parthenogens. G = sexual generations, P = parthenogenetic generations.

lengths of the vectors extending from the point of origin that track positional variation across parthenogenetic generations. The first of these factors is identical in both sexual and parthenogenetic organisms and simply measures the variation in net distances moved by individuals away from their point of origin. This is the type of dispersal envisioned by Wright when he formulated the neighborhood model. The second factor is generated by the random walk component that is the focus of this paper. This is a population metric that has no analog in sexually-reproducing organisms because of recombination. That is, the asexual parthenogenesis of rotifers creates a clonal continuity linking the genotypes of successive generations. It is this clonal continuity in combination with the directional variation produced by the random walks (Figure 1) that prevents genetic differentiation within neighborhood areas. Likewise, the concept of effective population size has no meaning as long as all reproduction is by parthenogenesis. Thus, for cyclical parthenogens, while dispersal will be occurring in every genera-

tion, effective population sizes are meaningful only for the sexual generations. The main point of this paper can therefore be summarized by the diagram presented in Figure 5. Neighborhood area remains constant under sexual reproduction, but increases with the number of parthenogenetic generations under cyclical parthenogenesis. That is, because of clonal reproduction, parthenogenesis in essence functions to increase dispersal distances. Consequently, when sexual reproduction occurs in cyclical parthenogens, the neighborhood area is equal in size to that of the last parthenogenetic generation rather than that of the last sexual generation.

We can envision situations in which both small and large neighborhood areas would be advantageous. For instance, as neighborhood area decreases, the population becomes more subdivided and has more inter-subpopulation genetic diversity. Such a structure potentially diversifies the evolutionary directions readily available to the population. In a changing environment, a subdivided population might be better able

to accommodate the changes by having subpopulations in existence that are adapted to the new conditions. However, the limited evidence available from field (King, 1972, 1977; Carmona et al., 1995; Gomez et al., 1995) and laboratory studies (Ito et al., 1981; King & Zhang, 1993; Miracle & Serra, 1989; Snell, 1979) suggests that rotifer populations tend to be composed of narrow-niched specialists exploiting only a small part of the entire annual environmental spectrum. In such circumstances small neighborhood areas would have little or no advantage and might even be disadvantageous because they would tend to truncate genetic variation by increasing random genetic drift.

We have shown that the dynamics of neighborhood areas are likely to be quite different in cyclical parthenogens and sexual organisms. As parthenogenetic reproduction expands neighborhood area, the neighborhoods of different subpopulations overlap. Regions of overlap may geographically define microhabitats in which interclonal competition and ultimately clonal succession will occur. Alternatively, overlap may simply result in a melding of formerly discrete neighborhoods thereby producing a new subpopulation and a new neighborhood area. In rotifers, neighborhoods will also receive input from the hatching of resting eggs from prior years. Although such changes to the genetic structure of the population potentially influence the ecological dynamics of the population, the spatial relationships of this influence are poorly understood in both theory and practice. For instance, do neighborhoods have optimum areas that vary under different ecological conditions? Both the genetic and ecological structures of populations are intimately related to geographical distributions. Neighborhood models offer the potential to address some of these relationships.

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