DISPERSAL IN THE WOOD FROG (*RANA SYLVATICA*): IMPLICATIONS FOR GENETIC POPULATION STRUCTURE

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Abstract.—Recapture of marked juvenile and adult wood frogs in five Appalachian Mountain ponds showed adults to be 100% faithful to the ponds in which they first bred, but approximately 18% of the juveniles dispersed to breed in ponds other than the one of origin. Effective population sizes were generally smaller than the population censuses and genetic neighborhoods had an average radius of 1,126 meters. Values of standardized genetic variance based on effective population size and mating success were relatively small. Genetic population structure estimated from the dispersal data suggested that ponds within about a 1,000 meter radius should show little genetic differentiation; ponds separated by a distance greater than 1,000 meters should experience little gene flow and show higher genetic differentiation. Wood frogs in these ponds do not show a meta-population structure as suggested for newts.

The maintenance of gene flow in the process of evolutionary differentiation is controversial. Species have been considered units held together by gene flow (Mayr, 1963) or units kept separate by natural selection (Ehrlich and Raven, 1969). In the former view, gene flow takes an active role maintaining a cohesive gene pool whereas in the latter view, gene flow is far less important in maintenance of a gene pool.

Gene flow estimates are essential to understand genetic differentiation over a geographic range. Organisms can be grouped into local demes or neighborhoods from which any two individuals could have originated with equal probability (Wright, 1943, 1969). For traits that are selectively neutral, gene flow rates of one migrant individual per generation are sufficient to prevent a significant proportion of the population to become fixed for different alleles (see Crow and Kimura, 1970). The geographic limits of the neighborhood are based on dispersal distance, therefore dispersal is important in the genetic population structure of organisms.

Gene flow has two components: (1) dispersal, movement of organisms away from their site of origin; and (2) reproductive success, the introduction of genes into a gene pool after dispersal has occurred. Rates of gene flow have been estimated by following dispersal movements of organisms. Such estimates of dispersal may overestimate rates of gene flow if dispersing individuals have

reduced reproductive success (Ehrlich et al., 1975; Endler, 1977). On the other hand, dispersal studies may underestimate actual or potential gene flow if the mechanism of marking individual organisms affects either survival or reproductive success.

In this paper, we estimate the genetic population structure of the wood frog *Rana sylvatica*. The wood frog is an ideal organism for such a study because populations of larvae develop in individual woodland ponds, metamorphose into juveniles, leave the ponds, and return in three or four years as mature adults to breed (Berven, 1982). Females mate with a single male and the vast majority of males mate with a single female (Howard and Kluge, 1985). Most studies of genetic population structure rely on electrophoretically determined gene frequencies from which gene flow is then inferred. However, electrophoretic studies may give incorrect estimates of gene flow due to small numbers of loci sampled or non-equilibrium distribution of allele frequencies. In this paper, we directly measure interpond dispersal rates and distances using marked populations of wood frogs and use these data along with survivorship and mating success information to infer gene flow and potential genetic population structure.

MATERIALS AND METHODS

Study Site.—This study was conducted in a group of five ponds located in the Shenandoah Mountains of Rockingham County,
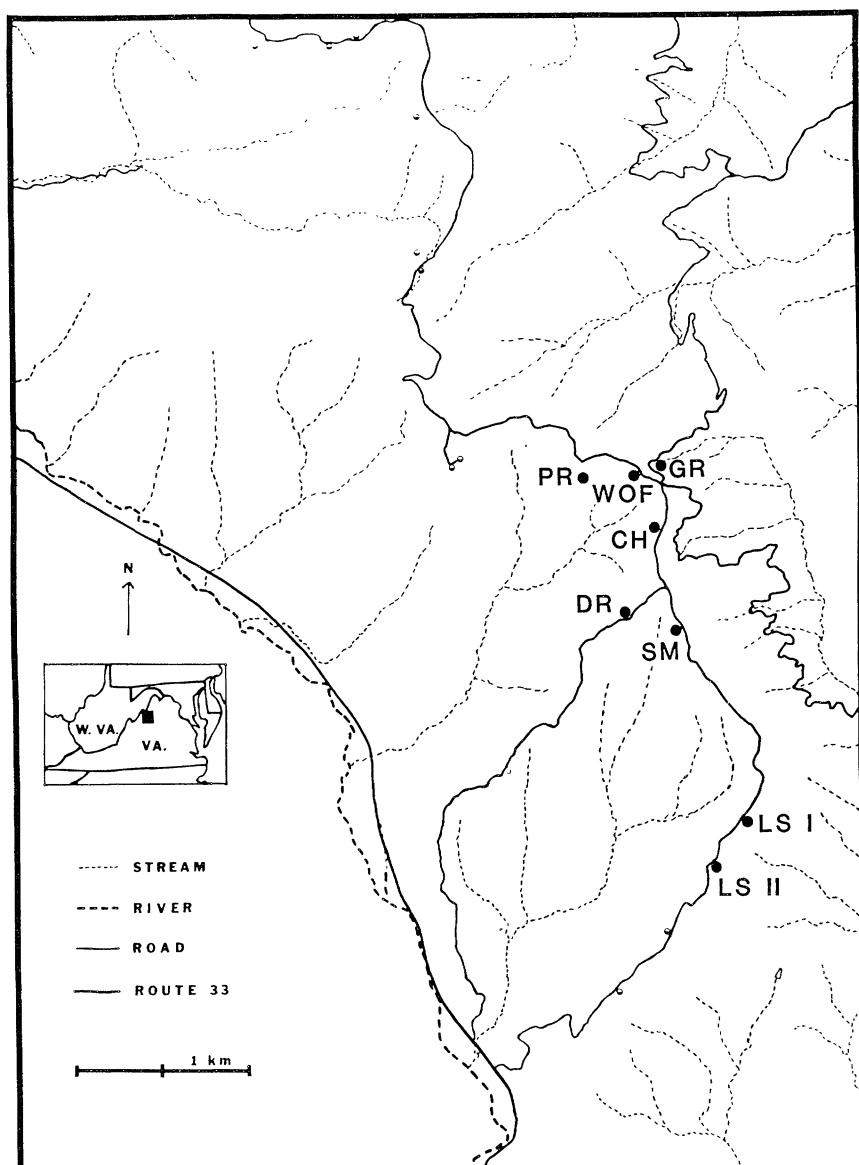
FIG. 1.   Map of ponds in the Shenandoah National Forest, Rockingham County, Virginia. Pond elevations in meters above sea level are PR 1,024, GR 1,018, WOF 1,030, CH 1,033, DR 1,114, SM 1,036, LS I 899, LS II 865.

Virginia. The ponds are located on a series of adjacent mountaintop ridges between an elevation of 865–1,114 meters (Fig. 1). The ponds referred to here as Pond Ridge Pond (PR), Gauley Ridge Pond (GR), White Oak Flat Pond (WOF), Clines Hacking Pond (CH), Dictum Ridge Pond (DR), and Second Mountain Pond (SM) are all circular, vary from 5–14 meters in diameter, and are up to one meter in depth. The relative lo- cation of the ponds is shown in Figure 1 and the actual distance between ponds is shown in Table 1. The distances between ponds were calculated using topographic maps and an opisometer. In those cases where the dis- tance between ponds could be traversed ei- ther by moving along a ridge top or crossing an intervening valley (i.e., DR–PR) we es- timated the distance as the average of the two values. A more detailed description of

TABLE 1. Distances (meters) between ponds.

	WOF	GR	KH	DR	SM
PR	680	1,160	1,530	2,530	3,780
WOF	—	264	850	1,850	3,100
GR		—	1,000	2,000	1,800
KH			—	1,000	1,250
DR				—	800

the ponds and surrounding habitat can be found elsewhere (Gill, 1978a, 1978b; Berven, 1982).

Adult and Juvenile Dispersal. — Wood frogs were intercepted by a continuous drift fence surrounding each pond. All breeding adult frogs encountered at the fence were marked by toe clipping with a unique pond-specific toe clip and an individual number. Monitoring of each pond from 1976 to 1982 provided an accurate determination of the number of breeding adults and also allowed us to screen for movement of breeding adults among ponds. Juvenile dispersal was determined from the recovery of juveniles marked in 1976 at PR and CH, and from PR and SM in 1977. Each juvenile was toe clipped to indicate the pond in which it underwent its larval period and the year of metamorphosis. Recovery of these juveniles as breeding adults between 1979 and 1982 provided a measure of juvenile dispersal. Specific details on these and other techniques used in this study are described elsewhere (Gill, 1978a, 1978b; Berven, 1982).

A negative exponential model [$y = a(10^{-bx})$] was used to estimate an overall dispersal curve for the wood frog populations (Wolfenbarger, 1946).

Measures of Effective Population Size. — Effective population size was estimated in three ways: the first method took into account the unequal sex ratio; the second, breeding behavior; and the third, yearly fluctuations in numbers of breeding frogs. Numbers of breeding males and females differed from year to year, therefore the formulation of $N_e = 4N_m N_f / N_m + N_f$ (Wright, 1938) was used for the first estimate. All female wood frogs entering a pond during the spring migration were gravid, and all mated with a single male. In addition, because of the typically male biased sex ratio and explosive breeding period (often lasting a single night), about half of the males did

not mate at all, and a very small number of males mated more than once. Therefore, a second estimate of effective population size was calculated as twice the number of females (females plus mates) when the sex ratio was male biased and as the sum of males and females when the population was female biased (some males mated more than once). The third estimate of effective population size accounted for the yearly fluctuations in population number (N_i) by calculating the harmonic mean of annual population sizes estimated by the first two methods (Wright, 1938). The above methods of estimating N_e may overestimate the actual effective population size because they do not take into account overlapping generations. However, the error using models assuming discrete generations is small (see Gill, 1978b) and, furthermore, only about 20% of adult wood frogs breed more than once so the effect of overlapping generations would be minimal. The estimates also do not consider variation in individual reproductive success and again may slightly overestimate the true values. Data on reproductive success were used to correct the overestimated effective population sizes.

Estimates of Genetic Neighborhood Area. — The genetic neighborhood of a deme was estimated by a circle with radius of 2 sigma, or two times the standard deviation of dispersal distance (Hartl and Clark, 1989).

Estimates of Potential Genetic Variation. — Standardized genetic variance (F_{ST}) was estimated using the number of migrating individuals and the formula of Wright (1940): $F_{ST} = \dfrac{1}{(4N_m + 1)}$. The F_{ST} estimate was used with information on survivorship and mating success to infer genetic population structure. This estimate of genetic variance is based on an island model and assumes equal dispersal probability between all ponds. If the ponds more accurately reflected a stepping-stone model the formula would underestimate the F_{ST} value.

RESULTS

Population Size. — The breeding adult populations were not stable. Population size fluctuated greatly both among years and among ponds (Table 2). For example, in 1978 the DR population was only 39, but

TABLE 2. Breeding population and effective population sizes of wood frogs at five Virginia ponds.

Pond	Numbers observed			Effective population size*		
	Males	Females	Sum	I	II	III
Pond Ridge						
1976	(203)	(250)	(453)	(448)	(453)	
1977	194	245	439	433	439	
1978	40	21	61	55	42	
1979	235	139	374	349	278	
1980	186	114	300	283	228	
1981	42	26	68	64	52	
1982	24	25	49	49	49	95 92
Clines Hacking						
1976	(180)	(200)	(380)	(379)	(380)	
1977	161	201	362	358	362	
1978	53	32	85	80	64	
1979	261	120	381	329	240	
1980	233	117	350	311	234	
1981	95	47	142	126	94	
1982	155	99	154	242	198	178 156
White Oak Flat						
1976	182	64	246	189	128	
1977	124	85	209	202	170	
1978	45	76	121	113	121	
1979	67	56	123	122	112	
1980	132	35	167	111	70	
1981	57	45	102	101	90	
1982	56	39	95	92	78	123 101
Dictum Ridge						
1976	84	43	127	114	86	
1977	—	—	—	—	—	
1978	23	16	39	38	32	
1979	217	366	583	574	583	
1980	90	96	186	186	186	
1981	24	6	30	19	12	
1982	93	20	113	66	40	54 38
Second Mountain						
1976	178	109	287	270	218	
1977	82	91	173	172	173	
1978	38	14	52	41	28	
1979	77	85	162	162	162	
1980	56	12	68	39	24	
1981	33	23	56	54	46	
1982	68	24	92	71	48	71 51
Overall	67	35	102	92	69	

* Effective population size I: $4N_m N_f/(N_m + N_f)$. Effective population size II: $2N_f$ if male biased sex ratio, $N_m + N_f$ if female biased sex ratio. Effective population size III: $1/N_e = 1/t(\Sigma 1/N_i)$; values are N_e(I) and N_e(II) respectively for each pond.

only one year later it reached a high of 583. Additionally, the number of juveniles produced at each pond also varied by three orders of magnitude among years and ponds (see also Gill et al., 1983) and total reproductive failure was not uncommon. Since juvenile wood frogs usually take three years to reach sexual maturity, the variation observed in adult populations among years was largely due to variation in juvenile recruit-ment (Fig. 2) indicating that each population was largely self-perpetuating.

Effective Population Size. —Effective population sizes were generally smaller than the observed numbers of frogs, especially when year-to-year fluctuations were taken into consideration (Table 2). Our calculation of effective population size based on sex ratio was usually smaller than that calculated from the unequal sex ratio formula
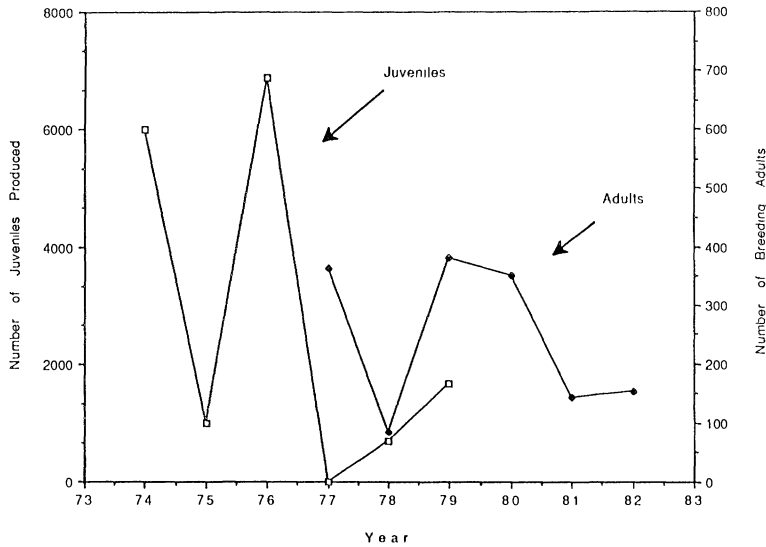
FIG. 2.   Numbers of juvenile and adult wood frogs at the Clines Hacking pond. Variation in population size of adults closely tracks the variation in juvenile cohort size three years earlier.

of Wright (1938). The overall effective population size per pond was relatively small showing the impact of occasional low population number on the harmonic mean.

Dispersal. — Throughout the duration of this study, not a single individual of the 11,195 marked adults migrated from one pond to another. Adult frogs all returned to the pond in which they were marked, suggesting that adult wood frogs are extremely faithful to their breeding ponds.

In contrast to the adults, 21% of the marked male and 13% of the marked female juveniles were recaptured as breeding adults in ponds other than those in which they underwent their larval period (Table 3). There was no significant difference between the numbers of dispersing males and females and, in general, there was close agree-

ment in the proportion of dispersers among juvenile cohorts (Table 3).

The average dispersal distance was 1,140 ± 324 (SD) meters and 1,276 ± 435 (SD) meters for males and females respectively (Table 4). There was no difference between sexes in average dispersal distance ($t = 1.29$, $df = 1$, $P > 0.40$). The longest distance moved by any juvenile was 2,530 meters by two individuals from the 1976 PR cohort. This rare long distance dispersal event accounted for the higher average dispersal distance for that cohort (Table 4). Dispersing wood frogs did not differ in age from nondispersers (Table 5). Dispersing males were significantly larger than nondispersing males (Table 6) although the dispersers were, on average, only 1 mm larger. Juveniles that dispersed to breed in other ponds were con-

TABLE 3.   Comparison of the number and proportion of dispersing wood frogs for each cohort of marked juveniles.

Cohort	No. marked	Males			Females		
		No. recaptured	No. dispersing	(Proportion)	No. recaptured	No. dispersing	(Proportion)
1976 PR	1,001	25	6	(0.24)	11	4	(0.36)
1976 CH	3,411	128	35	(0.27)	68	9	(0.13)
1977 PR	526	37	9	(0.24)	10	1	(0.10)
1977 SM	122	9	2	(0.22)	2	0	(0.00)
Overall	5,060	251	52	(0.21)	105	14	(0.13)

Chi-square male vs. female = 2.68, $df = 1$, $P > 0.05$.

TABLE 4. Mean dispersal distance (meters) from pond of larval development to breeding pond. Sigma is the standard deviation of dispersal distance including all zero values from nondispersing frogs.

		Males		Females		
Year	Pond	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	Sigma
1976	PR	6	1,573 ± 503	4	1,595 ± 561	756.4
1976	CH	35	1,051 ± 220	9	1,201 ± 207	465.1
1977	PR	9	1,271 ± 272	1	680 —	509.8
1977	SM	2	800 —	0	— —	800*
Mean		52	1,140 ± 324	14	1,276 ± 435	632.8
t (males vs. females) = 1.29, df = 64, P > 0.05						
Combined mean			1,169 ± 351, N = 66.			

* Standard deviation = 0 but value of 800 m is biologically meaningful for estimates of population structure.

sistently faithful as adults to the pond of dispersal in successive breeding seasons.

Dispersal curves were constructed from the proportions of dispersing juvenile wood frogs and distances they moved (Fig. 3). A least squares fit negative exponential line to the dispersal data [$y = (0.4392)10^{-0.000560x}$] accounted for 76% of the variation among cohorts and ponds. This regression had statistically significant goodness of fit (F test, $P < 0.01$).

Estimated Geographic Neighborhood Area. — The genetic neighborhood size for the 1976 PR cohort had a 2 sigma value of 1,513 meters and the neighborhood area (a circle with radius 2 sigma) was 7,192 hectares. The 1976 CH cohort had 2 sigma of 930 meters and neighborhood area of 2,719 hectares, while the 1977 PR cohort had 2 sigma of 1,020 meters, neighborhood area was 3,265 hectares. The 1977 SM cohort had two females that dispersed to DR (800 m, standard deviation = 0). Assuming a neighborhood radius of 800 m for DR, that deme had a neighborhood area of 2,011 hectares. The average neighborhood radius of these three cases was 1,266 ± 170 meters and yielded an average neighborhood area of 5,035 hectares.

Estimates of Potential Genetic Variation. — The overall effective population size

(N_e) was 69, using the formulae of Wright (1938). The overall dispersal rate (m) was 0.185 (66 dispersers of 356 recaptures, Table 3). Based on average effective population size and dispersal, F_{ST} = 0.019. This F_{ST} estimate was corrected for the fact that male biased sex ratios result in approximately 50% male mating success. The corrected overall dispersal rate was 0.112 (40 successful dispersers of 356 recaptures), and thus the estimated F_{ST} corrected for mating success was 0.031.

We also estimated F_{ST} using the dispersal curve (Fig. 3) and the average N_e estimate. The equation of the fitted dispersal curve was used to estimate proportion of wood frogs dispersing over a range of distances (0 to 4,000 meters). These estimated proportions of dispersers were then used with the average N_e value to calculate F_{ST} (Wright, 1938). The F_{ST} values were then plotted against distance (Fig. 4). Demes separated by the average neighborhood radius (1,266 meters, see above) were estimated to have an F_{ST} of 0.040, which closely approximates the F_{ST} calculated from the actual dispersal data.

DISCUSSION

Philopatry. — Adult wood frogs are extremely faithful to their breeding ponds.

TABLE 5. Comparison of the age of nondispersing and dispersing male and female wood frogs.

	Males		Females	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
Nondispersers	149	2.87 ± 0.41	70	3.56 ± 0.50
Dispersers	50	2.96 ± 0.35	14	3.50 ± 0.52
t (nondispersers vs. dispersers)	t = 1.39, df = 197 P > 0.05		t = 0.40, df = 82 P > 0.05	

TABLE 6. Comparison of size (snout–ischium length in mm) between dispersing and nondispersing three-year-old male (A) and three- and four-year-old female (B) wood frogs.

A) Males

Cohort	Nondispersers		Dispersers	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
1976 PR	18	56.9 ± 3.1	6	56.6 ± 2.9
1976 CH	93	55.8 ± 2.2	33	56.7 ± 2.1
1977 PR	7	60.4 ± 1.4	5	60.7 ± 1.6
Overall	118	56.2 ± 2.5	44	57.2 ± 2.6

t (nondispersing vs. dispersing) = 2.24, df = 160, $P <$ 0.05

B) Females

Cohort	Nondispersers		Dispersers	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
1976 PR	6	70.0 ± 4.2	4	67.6 ± 3.6
1976 CH	54	67.1 ± 5.3	9	66.4 ± 3.2
1977 PR	9	73.3 ± 2.2	2	67.5 ± 0.5
Overall	69	68.2 ± 5.3	15	66.9 ± 3.9

t (nondispersing vs. dispersing) = 0.9, df = 82, $P >$ 0.05

FIG. 3. Proportion of dispersing wood frogs versus dispersal distance with a least-squares fitted dispersal curve also plotted.

While adults appear to be 100% faithful, about 80% of juveniles remained philopatric and bred in the pond from which they metamorphosed. This was also shown from the fact that dispersed adults were recaptured in successive years only in the pond to which they had dispersed. Dispersal in the wood frog is distinctly age-specific, and is restricted to the juvenile stage. Age-specific vagility has been found in a variety of vertebrates (see Breden, 1987), and therefore, studies of dispersal based only on adults may seriously underestimate the actual migration rates.

Additional support for wood frog philopatry comes from two populations in Maryland separated by only 50 meters (Berven, 1982 and unpubl. data). In these ponds, 78% of male and 84% of female frogs breeding for the first time returned to the pond in which they underwent their larval development. In contrast, juveniles transplanted from Virginia to these Maryland ponds as part of a transplant study (Berven, 1982) returned as breeding adults to the two ponds in equal proportions (χ^2 = 2.25, df = 1, P > 0.10). The close proximity of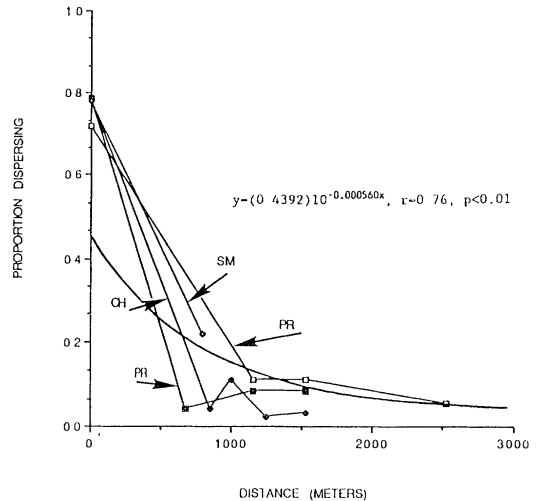 these ponds and the accuracy of resident individuals returning to their natal pond suggest that wood frogs possess an excellent homing ability.

Homing ability in anurans is well known and involves several different means of orientation including celestial navigation, visual cues, and olfactory cues (Ferguson and Landreth, 1966; Ferguson et al., 1965; Landreth and Ferguson, 1967; Twitty, 1964). Since the transplanted Virginia juveniles did not experience larval development or metamorphosis in the Maryland ponds, they appear to have lacked the cues needed to show philopatry.

Dispersal and Mating Success. — Although the majority of juveniles and all adults return to their pond of origin, the levels of dispersal observed in this study were sufficient to predict low levels of genetic differentiation among ponds. We estimate that the amount of among-population genetic variation should be only 3% of that which is potentially possible (fixation of all ponds for alternate alleles). Dispersal data often overestimate the actual rate of gene flow when data on reproduction is not available (Endler, 1979). In our study, juvenile dispersal resulted in migration of individuals among ponds that were detected as probable breeding adults and information on wood frog reproduction was incorporated with the dispersal data to better es-

timate gene flow and predict genetic population structure.

Field and laboratory experiments have shown that mate choice in the wood frog is size dependent; larger males are more successful in male–male competition for females, and males show a preference for large females (Berven, 1981). The 1-mm difference in size of dispersing males as compared to nondispersers was statistically significant (Table 6), however, the mating success differential between dispersing and nondispersing males based on 1-mm size difference is only 1% (see Berven, 1981). Therefore, the size difference between dispersing and nondispersing males is unlikely to have a strong biological impact on gene flow or population structure.

The sex ratio bias would be a more important factor determining male mating success. The predominately male biased sex ratio often resulted in male mating success of approximately 50%. Additionally, postmetamorphic wood frogs follow a Type II survivorship curve, in that they have an equal likelihood of mortality throughout their life span (Berven, 1990). All postmetamorphic frogs (juveniles and adults) disperse from the ponds in late spring and summer, returning to breed the next spring. Consequently, it is likely that dispersing and nondispersing individuals experience similar mortality.

Predicted Genetic Population Structure. — The life history data allowed the F_{ST} estimated on overall effective population size and overall dispersal rate to be corrected for reproductive success. An additional estimate of F_{ST} was made from the dispersal curve and the estimated radius of the genetic neighborhood, suggesting low levels of genetic divergence within the neighborhood of these ponds. These two estimates were quite similar (0.031 and 0.040 respectively), supporting our prediction of low genetic differentiation among ponds within the neighborhood radius. Furthermore, wood frog populations are arrayed along ridge-top ponds in the Appalachian Mountains approximating a stepping-stone model for gene flow. We suggest that ponds or groups of ponds separated by more than the neighborhood radius (1,071 meters) should show much greater levels of genetic differentia-
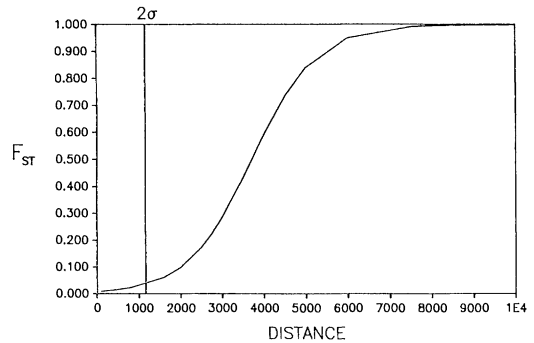

Fig. 4. Relationship between F_{ST} (standardized genetic variance) and distance (meters) among wood frog populations. Vertical line labeled 2 sigma is the average genetic neighborhood radius. F_{ST} increases rapidly beyond the average neighborhood radius.

tion than that estimated among the ponds within a single genetic neighborhood.

The estimated genetic neighborhood areas were very large, but because most frogs did not disperse, and those that did traveled very different distances, the sigma values are probably inflated. Since wood frog breeding habitat in this study was limited to mountain ponds, these estimated neighborhood areas are probably considerable overestimates of the true areas, and should be viewed with caution.

The dispersal data suggest that ponds within approximately a 1,000-meter radius should experience sufficient gene flow to inhibit local differentiation. However, it is possible for selection to maintain genetic differentiation in the face of considerable gene flow (Endler, 1973). Genetic variation in wood frog larval developmental patterns between mountain and lowland populations has been demonstrated (Berven, 1982) and directional selection implicated in the evolution of different life histories (Berven 1987). When the ratio of migration to selection is less than one ($m/s < 1$), local differentiation of populations will occur despite gene flow (Nagylaki, 1975). Within the limits of a wood frog neighborhood, selection would have to be rather intense ($s \geq 0.112$) to cause genetic differentiation, but outside the neighborhood limits selective coefficients could be much smaller and result in significant genetic diversity.

A study of dispersal and reproduction in the red-spotted newt (*Notopthalmus viri-*

descens) conducted in the same ponds by Gill (1978*b*) suggested a meta-population structure composed of a few ponds with high reproductive rates (reproductive centers) from which dispersers migrate to ponds characterized by very low reproductive success (reproductive sinks). Dispersal from the reproductive centers to the reproductive sinks maintained the populations of newts at a relatively constant size from year to year. In contrast to the newts, wood frogs do not maintain relatively constant population size (see also Gill et al., 1983), and our estimates of dispersal and gene flow suggest that wood frogs more closely approximate a model of genetic neighborhoods in which populations can respond to local environmental conditions yet remain linked by gene flow (Wright, 1932).

We view the wood frog populations of the Shenandoah Mountains to be ecologically individual units capable of independent response to varying local conditions, yet simultaneously acting as a single evolutionary unit linked together by gene flow. The relative magnitude of selection and gene flow will determine whether these populations evolve as a single unit or as several local demes. This view is very much a combination of the competing notions of species mentioned earlier: *Rana sylvatica* consists of populations (neighborhoods) held together by gene flow and, simultaneously, local units kept separate by the effects of natural selection. Given occasional long distance gene flow, the structure of wood frog populations closely approximates that assumed by Wright's (1932) shifting balance model of evolution.

LITERATURE CITED

BERVEN, K. A. 1981. Mate choice in the wood frog, *Rana sylvatica.* Evolution 35:707–722.

———. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica.* I. An experimental study of life history traits. Evolution 36:962–983.

———. 1987. The heritable basis of variation in larval developmental patterns within populations of the wood frog (*Rana sylvatica*). Evolution 41:1088–1097.

———. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71:1599–1608.

BREDEN, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad. Copeia 1987:386–395.

CROW, J. F., AND M. KIMURA. 1970. An Introduction to Population Genetics Theory. Harper and Row, Publ., N.Y.

EHRLICH, P. R., AND P. H. RAVEN. 1969. Differentiation of populations. Science 165:1228–1232.

EHRLICH, P. R., WHITE, R. R., SINGER, M. C., McKECHNIE, S. W., AND L. E. GILBERT. 1975. Checkerspot butterflies: A historical perspective. Science 188:221–228.

ENDLER, J. A. 1973. Gene flow and population differentiation. Science 179:243–250.

———. 1977. Geographic Variation, Speciation, and Clines. Princeton University Press, Princeton, NJ.

———. 1979. Gene flow and life history patterns. Genetics 93:263–284.

FERGUSON, D. E., AND H. F. LANDRETH. 1966. Celestial orientation of Fowler's toad, *Bufo fowleri.* Behavior 26:105–123.

FERGUSON, D. E., J. P. McKEOWN, D. S. BOSARGE, AND H. F. LANDRETH. 1968. Sun-compass orientation of bullfrogs. Copeia 230–235.

GILL, D. E. 1978*a*. The metapopulation dynamics of the red-spotted newt *Notopthalmus viridescens* (Rafinesque). Ecol. Monogr. 48:145–166.

———. 1978*b*. Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notopthalmus viridescens* (Rafinesque). Evolution 32:839–849.

GILL D. E., BERVEN, K. A., AND B. A. MOCK. 1983. The environmental component of evolutionary biology, pp. 1–36. *In* C. E. King and P. A. Dawson (eds.), Population Biology, Retrospect and Prospect. Columbia Univ. Press.

HARTL, D. L., AND A. G. CLARK. 1989. Principles of Population Genetics. Second Edition. Sinauer Assoc., Inc., MA.

HOWARD, R. D., AND A. G. KLUGE. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260–277.

LANDRETH, H. F., AND D. E. FERGUSON. 1967. Newts: Sun-compass and orientation. Science 158:1459–1461.

MAYR, E. 1963. Animal Species and Evolution. Harvard Univ. Press, Cambridge.

NAGYLAKI, T. 1975. Conditions for the existence of clines. Genetics 80:595–615.

TWITTY, V., GRANT, D., AND O. ANDERSON. 1964. Long distance homing in the newt *Trachia rivulans.* Proc. Nat. Acad. Sci. 51:51–58.

WOLFENBARGER, D. O. 1946. Dispersion of small organisms. Am. Midl. Nat. 35:1–152.

WRIGHT, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proceedings of the Sixth International Congress of Genetics 1(1932):356–366.

———. 1938. Size of population and breeding structure in relation to evolution. Science 87:430–431.

———. 1940. Breeding structure of populations in relation to speciation. Am. Nat. 74:232–248.

———. 1943. Isolation by distance. Genetics 28:114–138.

———. 1969. Evolution and the Genetics of Populations. Volume 2, The Theory of Gene Frequencies. University of Chicago Press.

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