Evolution, 46(4), 1992, pp. 930–938

THE DYNAMICS OF TWO HYBRID ZONES IN APPALACHIAN SALAMANDERS OF THE GENUS *PLETHODON*

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Abstract.-Two zones of i&gradation between populations of *Plethodon* have been studied for 18 and 20 years, respectively. The data consist of systematic scores of colors, made at least twice annually. Near Heintooga Overlook in the Balsam Mountains (Great Smoky Mountains National Park), the salamanders' cheeks are gray. Proceeding north toward the Smokies, there is increasing frequency and intensity of red color at two, four, and six miles. There has been no change in the scores at any location. The width of the zone and our failure to detect any change can be explained by assuming neutrality of the character and random diffusion during the probable time since contact between the two in&grading forms, which most likely took place after the Hypsithermal Interval, 8,000–5,000 BP. At Coweeta Hydrologic Laboratory in the Nantahala Mountains, *Plethodon jordani* and *P. glutinosus* hybridize at intermediate elevations. The lateral white spots of *glutinosus* decrease and the red on the legs of *jordani* increases with elevation from 685 m to 1,052 m. At the higher elevation, the proportion of animals scored as "pure" *jordani* declined significantly from 1974 to 1990, an indication that the hybrid zone is spreading upward. The rate of spread is too great to be explained by random diffusion, so selection for *glutinosus* characters is the best explanation. The rate of spread of the hybrid zone indicates that hybridization began 60-65 years ago, at the end of the time of intense timbering. Such human disturbances have caused hybridization in other organisms.

Key words.-Disturbance, hybrid zone, North Carolina, paleoecology, spreading rate.

Received February 4, 199 1. Accepted November 22, 199 1.

Beginning with the period of the evolutionary synthesis (Mayr, 1942, 1963), zones of intergradation have been regarded as important in understanding speciation and other aspects of the evolutionary process. It was recognized that steep clines could not be maintained without either selection against-the hybrids or some other selective force, such as that involving ecotones between ecologically different habitats to which the two intergrading populations were separately adapted (Mayr, 1963). Without these conditions, normal gene flow would spread the different genes of the two populations until the cline becomes nearly flat, its slope depending on the rate of gene flow and the number of generations since the process began.

In recent years, there have been significant advances in empirical studies (Littlejohn, 1965; Littlejohn et al., 1971; Littlejohn and Watson, 1985; Barton and Hewitt, 1981*a*, 1981*b*; Harrison and Arnold, 1982; Harrison, 1985, 1986; Arntzen and Wallis, 199 1; Szymura and Barton, 199 1), as well as in theory (Bazykin, 1969; Crosby, 1970; May et al., 1975; Endler, 1977; Barton, 1979*a*, 19796, 1983; Barton and Charlesworth, 1984; Slatkin, 1973, 1975, 198 1, 1985). This recent literature, reviewed by Barton and Hewitt (1985), and more extensively by Harrison (1990), has stressed the conditions necessary for the stability of hybrid zones, especially the importance of selection against hybrids. The evidence has included the absence or rarity of F_2 and backcross individuals (Arntzen and Wallis, 1991), or apparent linkage disequilibrium in the absence of chromosomal linkage, involving excess representation of parental genomes in the hybrid zone (Szymura and Barton, 199 1).

As noted by Harrison (1990), relatively few hybrid zones have been observed for more than brief periods. Most studies thus lack the time dimension, and interpretation has involved an assumption of stability.

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Nearly all of the studies that have spanned long periods have involved early and late observations, with few or none between (e.g., Rising, 1983; Moore and Buchanan, 1985; Hillis and Simmons, 1986; Turner, 1971; Amtzen and Wallis, 1991). Szymura and Barton (1991) provide an exception in the case of *Bombina* in eastern Europe, with data extending over a period of nearly 60 years.

We report observations made twice annually for 18 to 20 years on two zones of intergradation between large Plethodon salamanders in the southern Appalachians (Fig. 1). One of the zones is between two geographic representatives of *Plethodon jordani* that adjoin one another near the junction of the Great Smoky Mountains and the Balsam Mountains of North Carolina. In the Great Smoky Mountains, a range 77 km long, the *P. jordani* population consists almost entirely of red-cheeked individuals. Where the Smokies and Balsams come together, there is a narrow zone of intergradation, beyond which northeastward to the limits of the distribution of *P. jordani,* a maximum distance of 375 km, no specimens can be found with any red on their cheeks. Thus, the change between the two forms is relatively abrupt. The other zone involves *P. jordani* and *P. glutinosus* in the Nantahala Mountains; one of five restricted areas in which hybrids between these two species have been found. No hybridization has been detected in most areas of contact between these species throughout the southern Appalachians (Highton and Henry, 1970; Peabody, 1978). It is the exceptional nature of the hybridization that has caused most taxonomists to continue to recognize them as separate species (Highton and Henry, 1970; Peabody, 1978; Larson, 1984). Highton (1983) has recognized the geographic representative of *glutinosus* in the Nantahalas as *P. teyahalee.* We believe that the designation is unjustified (Hairston, in press).

These two hybrid zones have been under our observation for 18 and 20 years, respectively, and identical measurements have been made at least twice annually for 16 years. Other studies of the two species during the same period have given us further information about population density, population stability, population structure, interspecific competition, microdistribution and individual movements (Hairston, 1973, 1980*a*, 1980*b*, 1983*a*, 1983*b*; Hairston et al., 1987; Kneidel, pers. obs.; Nishikawa, 1985, 1990). For those unfamiliar with *Plethodon,* we emphasize the fact that all species are completely terrestrial, with direct development on land, and thus do not migrate to and from water.

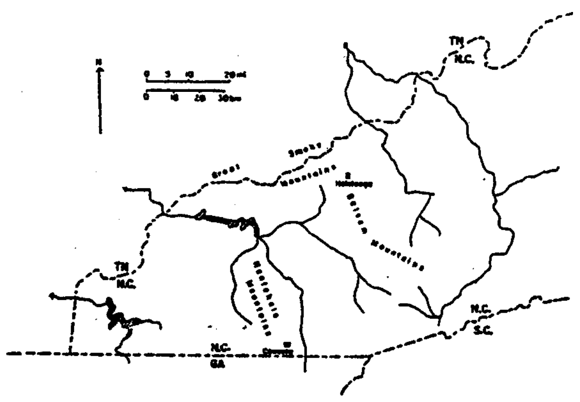

FIG. 1. Map of western North Carolina, showing the locations of the two hybrid zones. Solid lines are rivers; broken lines are state boundaries.

METHODS

The two zones of intergradation were observed as exercises for undergraduate classes. Two or three classes of 15 to 18 students visited the field sites each year. Most visits were in September; one was in June; and three were in April. The cline in the Great Smoky Mountains-Balsam Mountains area was found in 1973 and studied three times in 1973 and 1974, during which time the classification of colors was established. Observations started at Heintooga Overlook in the Great Smoky Mountains National Park and proceeded at odometer-measured two-mile intervals along the service road toward Round Bottom Camping Area (Fig. 2). The observations were made between 20:00 and 23:00 at night, when salamanders are active above ground, so as to avoid disturbing the habitat by turning logs and stones. At each stop, a class attempted to collect 10 or more specimens of *Plethodon jordani* (12 in 1990), and with one or two of us then scored the amount of red pigment on the cheeks of each specimen. We recognized five categories of color. 0 for none, 1 for small spots, 2 for a continuous line along the top of the

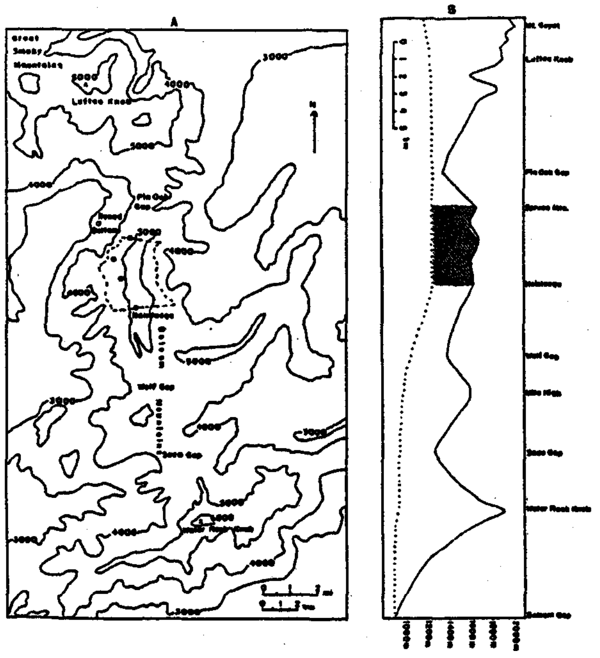

FIG. 2A. Contour map of the vicinity of Heintooga. Contour interval 1,000’ (305 m). Broken line outlines the hybrid zone.’ In this area, *Plethodon jordani* has not been found below 4,000’ (1,220 m) and is uncommon below 4,500’ (1,372 m), thus limiting the length of the hybrid zone. Open circle: Round Bottom; filled circles: collecting stops; x: major peak 2B. Profile of the area as viewed from the West. Vertical exaggeration 6: 1. Hatched area: hybrid zone; dotted line: approximate lower limit of *P. jordani*.

cheek but little else, 3 if the whole cheek was covered, and 4 if the red color extended onto the throat and could be seen from below. All specimens were returned to the forest after examination. Stops were made at 0, 2.0, 4.0, ‘and 6.0 miles, at elevations of 1,617 down to 1,434 m. The direct distance from the start to mile 6.0 on the road is 4,230 m. The plan was thus to observe 40 specimens on each visit to the area. On only 3 of 34 visits did we fail to find the requisite number, because of early cold weather, and we never obtained fewer than 32.

Observations in the Nantahala Mountains were conducted at the Coweeta Hydrologic Laboratory of the U.S. Forest Service. This area consists of two main east-facing watersheds. A forest service road ascends the mountain along each watershed. Hybridization of the two species at Coweeta was first observed by NGH in 1971 and .a classification of colors was established in 1972-1974. Our class exercises were carried out along Ball Creek Road, in the southern of the two watersheds. Salamanders were collected and scored in the same way as at Heintooga, except that two scores for coloration were recorded for each specimen. White spots, a characteristic of *P. glutinosus*, were recorded as 0 (none), 1 (very few spots along the sides or cheeks), 2 (spots along the sides but none on the back), and 3 (many spots on the sides and at least a few on the back). Red legs, a characteristic of *P. jordani* in the Nantahalas, were recorded as 0 (none), 1 (very small spots of red on the forelegs), 2 (red on the forelegs but little if any on the hindlegs), and 3 (the proximal parts of both forelegs and hindlegs fully or mostly red). During each visit, stops were made according to elevation. We began at 685 m and used an aneroid altimeter to determine each subsequent stop at 91.5 m (300’) intervals until we reached 1,052 m, making a total of five observations. On only two ‘occasions out of 35 did we fail to obtain the planned 50 specimens.

TABLE 1. Proportional distribution of color of *Plethodon jordani* along the Heintooga-Round Bottom Road. Data from all field trips combined.

	Distance from Heintooga (miles)			
	0	2	4	6
N:	366	373	450	470
Amount of red:				
1	0.997	0.861	0.120	0.006
2	0.003	0.019 0.121	0.324 0.278	0.215 0.072
3			0.238	0.402
4			0.040	0.304

The methods used to obtain other information on these salamanders are described in the papers cited above.

OBSERVATIONS

Two Geographic Representatives of Plethodon jordani

North of Heintooga, our studies revealed no consistent change in scores for coloration at any collecting location. Regressions performed on the arcsine percent of each score for red at each location on the number of years since the start of the study revealed only one statistically significant relationship (slope = -0.011 and r^2 = 0.13). As only one specimen out of 360 (0.003) at the Balsams end of the transect had a tiny fleck of red on one cheek, and only 3 out of 470

TABLE 2. Changes in color characters with altitude along the Ball Creek Road, Coweeta Hydrologic Laboratory (38 visits, 1974-1990). Numbers in the body of the table are proportions of specimens with each combination of colors at the respective altitude.

Altitude (m)	N	Color R3 > W	R2 > W	R1 > W	R - W	W1 > R	W2 > R	W3 > R
> 1,067	37	0.378	0.297	0.216	0.108			
1,052	447	0.340	0.348	0.227	0.075	0.002		
961	521	0.155	0.271	0.274	0.253	0.038	0.008	
869	464	0.069	0.168	0.297	0.331	0.100	0.034	
778	339			0.014	0.108	0.280	0.345	0.251
685	319				0.012’	0.046	0.271	0.670

Note: R3 > W: Red 3, White 0; R2 > W: Red 2, White 0, or Red 3, White 1; R1 > W: Red 1, White 0, or Red 3, White 2, or Red 2, White 1; R = W: Red 3, White 3, or Red 2, White 2, or Red 1, White 1, or Red 0, White 0; W1 > R: White 2, Red 1, or White 3, Red 2, or White 1, Red 0; W2 > R: White 3, Red 1, or White 2, Red 0; W3 > R: White 3, Red 0.

(0.006) at the Smokies end of the transect lacked red, we are confident that our stations at 0 and 6 miles are close to the edges of the zone of intergradation, the width of which is thus close to 4,230 m. It is clear that if there has been any change in the distribution of colors during the 18 years of our observations, we have failed to detect it. Table 1 summarizes the proportions of scores at each location for all years combined.

Hybridization between P. **glutinosus** *and* P. **jordani** *at Coweeta*

A transect along Ball Creek Road in 1972 revealed a cline from "pure" *glutinosus* to "pure" *jordani* throughout the range of elevations between 685 m and 945 m, above which no further change was found (Hairston, 1973). The subsequent detailed analyses of this transect have confirmed these initial observations (Table 2). In every year, there has been a gradual change in color with elevation, with the greatest variation among individuals at intermediate elevations, as expected in a hybrid zone. Peabody (1978) reported a transect of collections along the Ball Creek Road, which were analyzed for genetic variation in the seven proteins that distinguish between the two species. The change in frequencies was closely similar to the changes in color reported here.

The summation of scores for colors obscures an interesting point. Despite the data being taken by the same people as on the Heintooga-Round Bottom Road, the results were not constant from the start of the class exercises in 1977 to the present. Regressions show two trends, one of which is statistically significant (Fig. 3). The proportion of salamanders rated as either 3 red 0 white or 2 red 0. white ("pure" *jordani*) at 1,052 m (3,450') declined significantly between June 1974 and September 1990 ($df = 33$, $P <$ 0.000 1, slope = -0.0166, r^2 = 0.504). The proportion-rated 3 white 0 red or 2 white 0 red ("pure" *glutinosus*) at 685 m (2,250') also declined over the same period ($df = 33$, $P = 0.13$, slope = -0.009, r^2 = 0.071). The data for the latter trend are too variable to give a statistically significant result; so we cannot claim that there was a real change at the lowest elevation. This analysis shows that the hybrid zone spread at least upward during 16 ½ years of intensive study. Unconscious systematic bias of the participants in this study from year to year seems especially unlikely, in view of the consistency at the other location.

In 1971, a transect was made in the adjacent watershed along Shope Creek Road at elevations from 685 m to 1,281 m. We did not find a regular change from "pure" *glutinosus* to "pure" *jordani* as we ascended. White spots decreased and red on the legs increased up to an elevation of 915 m, but from there to 1,113 m the trends were reversed. Above that elevation, the original trend was again found.

Some observations made by one of us (KAK) in 1977 suggest that environmental factors affect the distribution of *glutinosus* along Shope Creek Road transect The reversal of trends at intermediate elevations along the road was confirmed. Interpretation of this transect is complicated because the road leaves the moist creekside habitat to follow a dry ridge at intermediate elevations. To separate the effects of habitat and elevation, four new transects each fol-

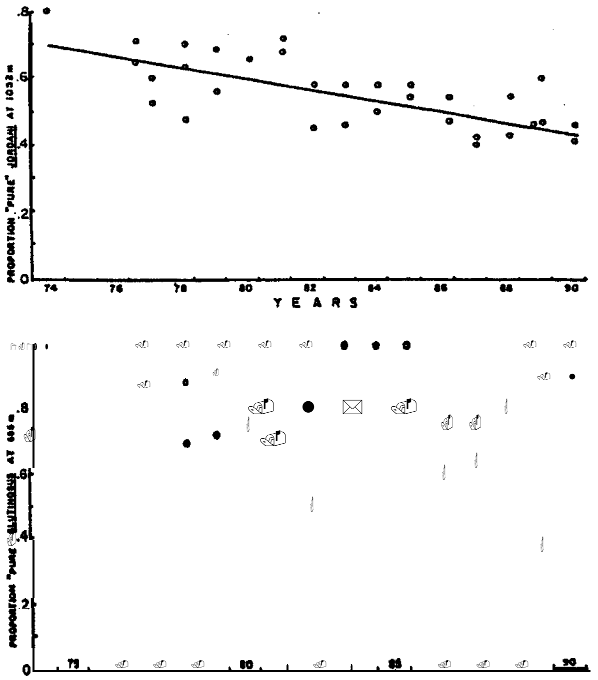

FIG. 3. Change in proportions of "pure" *Plethodon jordani* at 1,052 m and "pure" *P. glutinosus* at 685 m on the Ball Creek Transect, Coweeta Hydrologic Laboratory, between 1974 and 1990. Solid symbols represent 2 identical observations. See text for explanation of "pure," and for statistical analysis of the data.

lowed a single habitat from low to high elevation. The scores for coloration along each transect showed regular changes toward *jordani* at successively higher locations, but on the dry ridges scores were more like *g&inosus* than on the transects in wetter habitats at comparable elevations. Thus *glutinosus* traits increase on dry ridges away from streams for any given elevation.

DISCUSSION

The Probable Duration of the Clines

Heintooga-Round Bottom.—The steepness and apparent stability of this cline could be explained in several possible ways (Moore, 1977; Barton and Hewitt, 1985; Harrison, 1990). (1) If the traits involved are neutral or nearly so, the width of the cline would reflect the rate of gene diffusion because the two geographic races of *P. jordani* came into contact after a period of separation. (2) Hybrids could be confined to a narrow zone of intermediate habitat where they have greater fitness than parental types. Or (3) the hybrid zone could represent a dynamic equilibrium between hybrid inferiority and migration from adjacent parental populations. Of these, the first involves the simplest mechanisms and thus constitutes an appropriate null hypothesis.

The most obvious cause for the postulated separation is climatic change during the Pleistocene or Holocene. Molecular data suggest that the differentiation of *jordani* into geographic races apparently occurred at, least as early as lower Pleistocene. The red-cheeked form, currently confined to the Great Smoky Mountains, is as different in allozymes from the other forms of *jordani* as *jordani* is from the local form of the *glutinosus* complex (Peabody, 1978). Using Peabody's data, and assuming a molecular clock, Larson (1984) estimated that the two species separated 2-3 × 10^6 years ago. Thus, there have probably been many isolations and contacts among the geographic forms of *jordani.* We need be concerned only with the most recent isolation and contact.

The location of this zone of intergradation on a ridge joining higher peaks (Fig. 2B) suggests that isolation on those separate peaks during a warmer period was followed by spread along the ridge by both forms. Contact would thus have resulted sometime after the beginning of a cooler and moister period The requisite cooler period is, however, unlikely to have been a glacial maximum. There is substantial geological evidence that the timberline was no higher than 1,300 m as far south as the Great Smoky Mountains during the maximum Wisconsin glaciation 18,000–14,000 BP (Clark, 1968; Michalek, 1968). The woodland salamanders would have been confined below that level, and the mountain ranges would have been barriers, rather than the refugia that they are now (Deevey, 1949). An alternative possibility is that secondary contact a short distance North of Heintooga began quite recently. It is possible that *jordani* was confined above its present zone of intergradation during the Hypsithermal Interval between 8,000 and 5,000 BP. The warmer climate apparently forced the lower limit of the boreal spruce-fir forest nearly 400 m higher than it now exists (Whittaker, 1956), and the lower limits of other distributions would also have been raised. As a consequence, *the two* forms *of jordani* could have been isolated from each other on the peaks higher than 1,750–1,800 m. With the cooling trend after 5,000 BP (Delcourt and Delcourt, 1980), the red-cheeked and gray-cheeked isolates would have come into contact eventually, on the ridge between Soco and Pin Oak Caps. The null hypothesis above assumes random diffusion of genes for red cheeks since then.

Is this hypothesis consistent with the probable spread of the two populations as they interbred? Under the assumption of neutrality of characters, the time since the two forms came into contact can be calculated from the equation derived by Endler (1977):

$$T = 0.35(w/L)^2$$

where T is the number of generations to create a cline w meters wide with a rate of gene flow of L meters per generation. The width of a cline is defined as the distance between the gene frequencies 0.2 and 0.8. Lower and higher frequencies constitute the tails of the distribution, the use of which might invalidate the use of the equation. Hairston (19833) calculated the mean generation time of *P. jordani* as *9.78 years;* and the gene flow rate can be estimated from the diffusion constant, D.

Berg (19 8 3) gives the following equation for one-dimensional random walk:

$$s^2 = 2\,Dt$$

where s^2 is the variance in movement per time unit; D is the diffusion constant; and t is time. The variance in movement found by Nishikawa (1985, 1990), using a mark-release-recapture method over an entire season of activity, and averaged for four age and sex classes was 2.9 m for average intervals of 17.2 days, or 117.85 of the active season of 135 days, as determined by Hairston (pers. obs.). Solving, D is 0.084 m per day, or 11.38 m per season of activity. Gene flow per generation would thus be 111.3 m.

We can obtain maximum estimates for w and T if we assume that the cline extends the entire way from 0 to 6 miles, the direct distance between which is 4,230 m. In that case, the solution to Endler's equation gives the time required to reach the present width of the zone of intergradation as 4,950 years. Allowing for the fact that the unknown width from gene frequencies between 0.2 and 0.8 (Endler's requirement) is surely less than 4,230 m, the time is consistent with contact following isolation during the Hypsithermal.

As the nearest peaks high enough (2,0 19 m or 1,901 m to the North, 1,919 m to the South) to serve as refuges are 11.9 km and 16.1 km, respectively, from the center of the zone of intergradation (Fig. 2), it might be objected that there would not have been sufficient time for the two color morphs to reach each other by random walk. However, intraspecific competition 'would presumably slow movement compared with the rate of spread before contact. For example, the present distribution of *P. glutinosus* extends to 240 km north of the maximum extent of the Wisconsin ice sheet, and must have reached that limit since the appearance of forests 14,000 BP. The rate of spread into habitat unoccupied by conspecifics was thus 17 m per year. At that rate, the two forms of *jordani* would have made contact after at most 900 years, leaving more than 4,000 years to achieve the present width of the cline.

These calculations thus suggest that the features of this hybrid zone are consistent with neutral diffusion following secondary contact. We cannot conclusively exclude other mechanisms in this case. However, the abundance of all intermediates in coloration in the center of the zone suggests many F_2 and backcrossed individuals and argues against any heterozygote disadvantage. In addition, there is no readily apparent environmental gradient or trough in population densities that might constrain the location of this zone. We thus conclude tentatively that these two forms of *P. jordani* exemplify neutral or nearly neutral diffusion since contact some 4,000 years BP.

Coweeta.-Although the cline at Heintooga and our failure to detect any change in it can be accounted for by the assumptions of neutral diffusion, such is not the case at Coweeta. The upward spread of the zone of hybridization has been much too rapid to have been accomplished solely by movements of the salamanders. The observations of Nishikawa (1985, 1990) show that *glutinosus* is even more sedentary than *jordani.* The mean'distance between captures was 1.095 m, and ranged from 0.8 1 m for two-year-olds to 1.69 m for adult females over a mean period of 14.4 days. Variances ranged from 0.245 to 3.15, and averaged 1.73 m. Extrapolation of the regression in Figure 3 gives 1997 as the year in which the proportion of "pure" *jordani* at 1,052 m is expected to have declined to the overall average at 96 1 m. The direct distance between points at elevations of 961 and 1,052 m is 477 m, which would require the average *glutinosus* 854 years to cover by the assumption ofrandom walk. This time is about 43 times longer than the observed change predicts. The assumption of neutrality is therefore rejected, and we conclude that the *glutinosus* characters have increased their proportion at the higher elevation as a result of either hybrid superiority or a selective advantage for *glutinosus.*

Our studies in the Shope Creek watershed also suggest that selection might influence the distribution of *glutinosus* characters in this area. In the hybrid zone, the drier ridges favor *glutinosus* traits, which are found at higher elevations- there than elsewhere. These results are consistent with the general distribution of the two species, withjurdani on higher, cooler, and moister mountains, and *glutinosus* in lower, warmer, and drier valleys.

Thus, natural selection in the Nantahalas appears to explain the upward spread of hybrid traits at a rate faster than the animals themselves could move. An unexplained feature of these observations is the apparent linkage of color characters with physiological traits that would presumably be subject to selection. It is a fortunate circumstance for us, because without the linkage, detecting the effects would not be possible with the methods that we have used.

The rate of spread of *glutinosus* traits furthermore suggests that hybridization itself is of very recent origin. Assuming that the hybridization began at about the midpoint of the present hybrid zone, which is approximately 3,000 m wide at Coweeta, and assuming that the traits spread at the same rate as we have observed, the present width of the zone would have been reached in 63 years (477 m in 20 years or 1,500 m in 63 years). The calculated time for achieving the present hybrid zone indicates that its beginning coincided approximately with the end of intense lumbering, as suggested by Highton and Henry (1970). Records at the Coweeta Hydrologic Laboratory show that although settlement of the area began as early as 1840, heavy lumbering occurred mostly in the period between 1903 and 1923. More exact estimates of the coincidence are not possible because we do not know the altitudinal width of the zone of overlap prior to hybridization. It is quite likely that the hybrids found between *Plethodon glutinosus* and other isolates of *P. jordani* are of equally recent origin. Recent hybridization between well-differentiated species of plants (oaks, Muller, 1952); (fish, Hubbs, 1955), (snow geese, Cooke et al., 1988) and other groups have also been associated with human disturbance.

These analyses have demonstrated that in spite of a superficial similarity, the two clines that we have studied have different origins and very different dynamics: Carefully repeated observations over many years were essential to the demonstration.

ACKNOWLEDGMENTS

We thank successive officials of the Great Smoky Mountains National Park for permission to carry out the study at Heintooga, and we thank especially D. DeFoe for showing NGH the road and other cooperation. We thank Dr. W. Swank for permission to work at Coweeta. The O'Bryan family kindly welcomed us to their summer home after the night sessions, making the field 'trips a pleasure for us and hundreds of students. Some of the classes used the facilities of the Highlands Biological Station. Finally, we thank the many teaching assistants, who patiently recorded the scores.

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