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PATTERNS OF COLOR POLYMORPHISM IN THE CRICKET FROG, *ACRIS CREPITANS*, IN KANSAS.—The cricket frog, *Acris crepitans*, is a wide ranging semi-aquatic hylid frog which displays polymorphism for three vertebral stripe color morphs: gray, green and red. *A. crepitans* has been of interest in studies of color polymorphism because it is distributed over much of the eastern half of the United States and therefore encounters extreme environmental conditions both seasonally and geographically. In this report I examine temporal, geographic and allozympic patterns of color polymorphism in *A. crepitans* in a western segment of the range, Kansas. I also compare color polymorphism in populations from pond and stream habitats in eastern Kansas.

Materials and methods.—Sixteen sampling localities in Kansas were chosen for study. Thirteen were distributed along a 39°N latitude transect within the Kansas River drainage from the western to the eastern border of Kansas (Fig. 1). Three southern localities were in the Arkansas River system and provide comparison between drainages. Stream sampling localities were grouped into four geographical areas—west-

ern, central, eastern and southeastern Kansas (Fig. 1). In addition to stream localities, pond localities were also included in the eastern group.

Frogs in eastern Kansas were collected every 4–6 wk from late 1978 through 1980. Western and central Kansas localities were sampled once in the fall of 1979 and 1980 and spring of 1980. The southeastern Kansas localities were sampled once. Frogs were caught by hand along the water's edge. Standard time allotments and sample areas (approx. 100 m × 1.5 m) were covered for each locality. At Womaker Pond I censused frogs monthly from fall 1981 to fall 1982 by walking slowly around the pond once and tape recording the various color morphs seen.

Estimation of adult breeding population size for each eastern locality was calculated from May or June of 1980 samples by using capture rate/unit area, capture efficiency and total habitat area occupied by the frogs (for streams this was calculated for a 1 km reach). Since breeding adult sex ratios were not significantly different from 50:50 (Table 1) the effective population size is the estimated adult population size.

Color morph, age (adult or juvenile) and sex were recorded from dissected anesthetized frogs. Heart, blood and liver tissues were removed for electrophoretic analysis. Allelic frequencies of seven polymorphic loci (Gorman, 1983), LDH, GPI, SOD, LAP, aNAC (alpha-naphthyl acetate

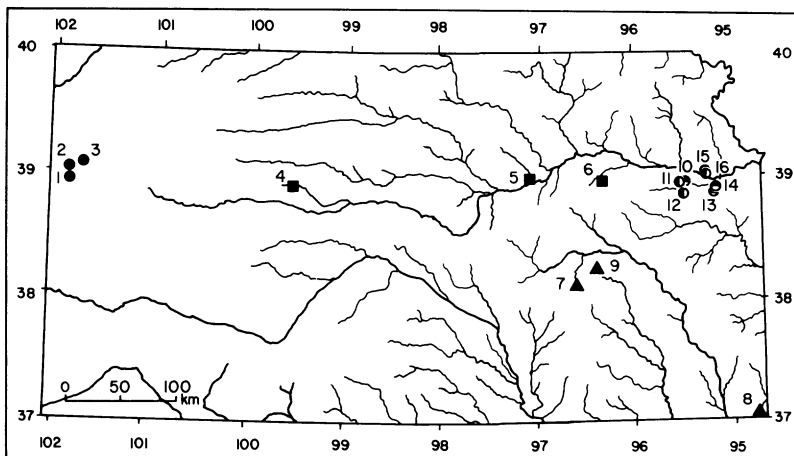


Fig. 1. Sampling localities in Kansas of *Acris crepitans*. ● denotes the western Kansas group, ■ the central, ▲ the southeastern and ○, ● the eastern ponds and streams, respectively. For locality names corresponding to numbers, see Table 1.

TABLE 1. ADULT COLOR MORPH FREQUENCIES AND POPULATION PARAMETERS OF *Acris crepitans* FOR INDIVIDUAL LOCALITIES AND GEOGRAPHIC AREAS. Data are from May–July 1980 samples of adults. N is sample size. Averages are weighted for sample size.

Locality	Number designation	N	% gray	% green	% red	% males	Effective pop. size
Western							
Willow Ck.	1	4	1.000	0	0	.50	
Goose Ck.	2	21	.905	0	.095	.57	
Lake Ck.	3	66	1.000	0	0	.50	
		91	.978	0	.022	.52	
Central							
Big Ck.*	4	49	1.000	0	0	.37	
Chapman Ck.	5	25	.520	.120	.360	.68	
Mill Ck.	6	11	.818	.091	.091	.55	
		85	.835	.047	.118	.48	
Southeastern							
Cottonwood R. (Thurman Ck.)	7	28	.714	0	.285	.64	
Shoal Ck.	8	7	.714	.143	.143	.43	
Jacobs Ck.	9	7	.571	.286	.143	.29	
		42	.691	.071	.238	.55	
Eastern							
Collins Pond**	10	8	.750	.250	0	1.00	75
Rock Ck.	11	35	.714	0	.286	.71	1280
Deer Ck.**	12	25	.960	0	.040	.68	667
Womaker Pond	13	90	.604	.209	.187	.51	1440
Quarry Pond	14	19	.790	0	.210	.63	608
Fish Farm Pond	15	23	.435	.304	.261	.52	6432
Mud Ck.	16	25	.600	.160	.240	.48	2660
		226	.664	.142	.195	.58***	

* Fall samples (juveniles).

** Proportions of color morphs in 1979 are not significantly different.

*** Not significantly different from .50.

esterase), UMEST (4-methylumbelliferyl acetate esterase) and GPRO (general protein) were determined for each color morph at each eastern locality except Deer Creek.

Results.—Four eastern localities had sufficient sample sizes for statistical analyses of temporal variation. Seasonal variation in color morph frequency revealed an inconsistent pattern (Fig. 2). Independence of season (collection month) and color morph was tested using contingency Chi-square analysis for each year (1979 and 1980) for each locality. (Due to the low frequency of green morphs at Quarry Pond and Rock Creek, comparisons were between gray and nongray.) Only 1 of 8 Chi-square values was significant, indicating that seasonal factors do not influence color morph frequency.

Frequencies were averaged for each year for each locality and independence of year and color morph was tested by Chi-square. No significant differences were found between years for any of the four eastern localities, indicating that color morph frequencies are temporally stable within localities.

To reduce variation introduced by annual and generational effects, only samples of May–July 1980 adults were examined for geographic variation (Table 1). Averaged gray and nongray proportions differed significantly between ponds and streams ($\chi^2 = 10.20$, $P < .005$), due primarily to a higher frequency of the green morph in ponds (Table 1). Two exceptions were Quarry Pond, which lacks the green morph and Mud Creek which had a higher proportion of the green morph than other stream localities. How-

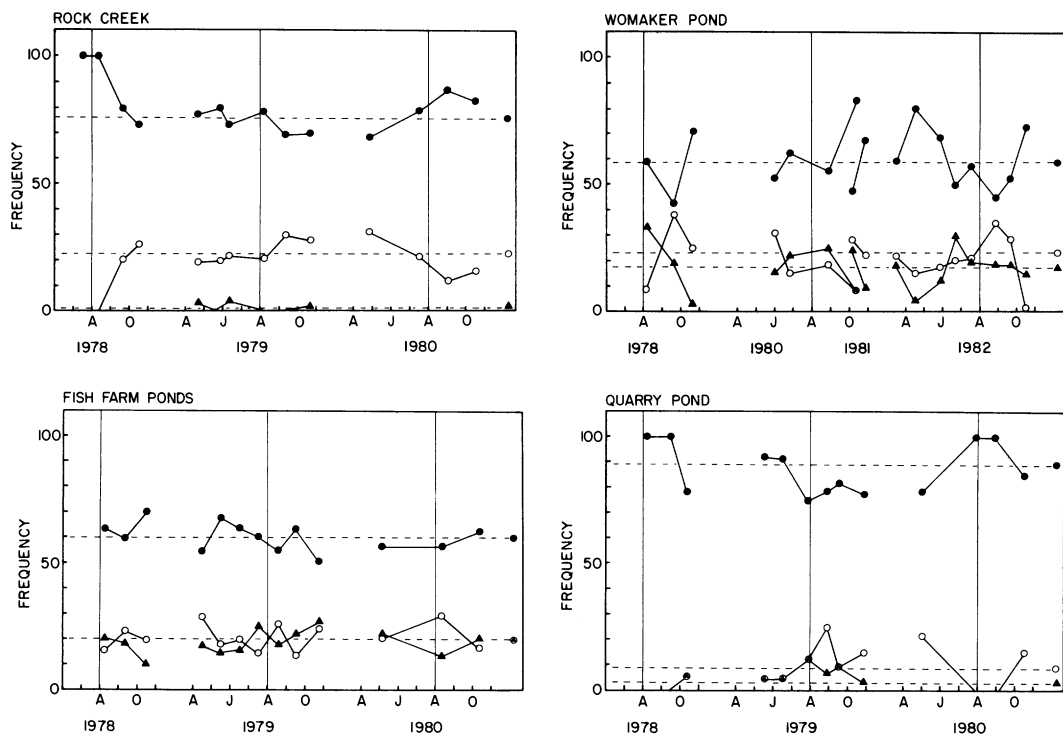


Fig. 2. Temporal patterns of color polymorphism in *Acris crepitans* at four eastern Kansas localities. ● denotes the gray morph, ○ the red and ▲ the green. The dashed line followed by a symbol indicates the average frequency over 3–4 yr for the corresponding color morph. Only months in which frogs were collected (April–Nov. for each year but 1978) are indicated.

ever, these two localities are unusual in that Quarry Pond has large exposed mud flats and little littoral vegetation and Mud Creek is adjacent to a large complex of fish farm ponds.

Heterogeneity of allelic frequencies among the three color morphs (or gray and nongray for Quarry Pond and Rock Creek) was tested for each locus using a heterogeneity Chi-square analysis (Workman and Niswander, 1970). Four of 42 (7 loci, 6 localities) analyses indicated significant heterogeneity among color morphs at 3 loci, GPI (for two localities), SOD and GPRO. When allelic frequencies for each color morph were averaged for all six eastern localities, significant heterogeneity among color morphs was found for two loci, LDH and GPRO. The lack of a definite pattern of genetic differentiation among color morphs indicates that morphs do not differ allozymically either within or between localities and suggests that color morphs are randomly breeding.

The color morph frequencies exhibited a general clinal pattern of variation across Kansas (Table 1). The gray morph increased to near

fixation westward while the green morph decreased. The red morph was less clear, but generally decreased westward. However, several localities deviated from the overall clinal pattern. Proportions of gray and nongray morphs in the four geographic areas were significantly different (χ^2 contingency = 38.27, $P < .001$ for all localities; χ^2 contingency = 22.21, $P < .001$ for stream localities only), but not when the western group, with its much higher frequency of the gray morph, was eliminated from the analysis.

Discussion.—Pyburn (1961) noted that over a 3 yr period the color morph frequencies of *A. crepitans* in Texas varied seasonally as a result of changing substrate colors. Subsequent studies of the entire range (Nevo, 1973) and of subregions, e.g., Indiana (Isaacs, 1971), Illinois (Gray, 1983) and Kansas (Burkett, 1969; this study) have found no statistically significant seasonal patterns. Though these later studies contrast with the Texas study, Gray (1983) suggests that because of differences in life history throughout the range of *Acris*, various factors

such as predation or physiological advantage may have different impacts on local populations. At least in the western (Kansas) and northern (Illinois) parts of the range, predation does not appear sensitive enough to track seasonal substrate changes.

Predation has been proposed as a mechanism responsible for creating or maintaining color morph frequency differences among localities for *Acris* (Pyburn, 1961; Milstead et al., 1973; Nevo, 1973), although there is little direct evidence of this (Gray, 1978). Since Kansas ponds are manmade, pond-dwelling *Acris* necessarily came from stream stock. It is unlikely that in the absence of some selective agent, such as predation, the rare green morph be consistently in a higher proportion in pond localities and that both pond and stream localities have stable color morph frequencies. Gray (1983, 1984) demonstrated that significant differences in morph frequencies in Illinois can occur within and among localities due to genetic drift if effective breeding sizes are small. However, color morph frequency differences between Kansas ponds and streams cannot be accounted for by genetic drift since their effective population sizes are sufficiently large and this is indicated by temporally stable color morph frequencies.

Pyburn (1961) and Nevo (1973) found a correlation in the regional color morph frequency with gross climatic gradients. The westward increase in the gray morph frequency was associated with increasing aridity and only secondarily with increasing gray substrates (Nevo, 1973). A summarization of Nevo's (1973) genetic crosses shows that 23/23 of the green morphs and 32/34 of the red morphs were heterozygous. If similar proportions were heterozygous in Kansas, then alleles for the green and red morphs are quite rare. Even though the geographic pattern of color morph variation in Kansas can be correlated with climatic variables (Gorman, 1983), a more likely explanation is that the rare alleles for the green and red morphs were lost by chance with dispersal westward up the Kansas River drainage. This westward loss of the rare alleles in Kansas is concordant with patterns of allozymic loci (Gorman, 1983). Thus, gross climatic factors may be irrelevant. Gray (1984) also proposes that at least in the northern populations (Illinois) chance may override the effect of natural selection in populations with small effective breeding sizes.

Although allozymic differences were found among color morphs in Kansas, the lack of a

general pattern suggested no physiological differences or mating preference which might account for geographic patterns of color morph frequencies. This contrasts with Nevo's (1973) results of physiological differences between red and gray morphs from Texas, but is in agreement with results of Gray (1977, 1978, 1983) for Illinois *Acris* morphs. Frogs from pond and stream habitats have been found to differ in genetic composition, primarily at the LAP locus (Gorman, 1983). That color morphs do not differ significantly at this locus indicates that color morph selection is independent of the rest of the genome.

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WENDY L. GORMAN, *Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045. Present address: Department of Virology and Molecular Biology, St. Jude Children's Research Hospital, 332 N. Lauderdale, PO Box 318, Memphis, Tennessee 38101. Accepted 11 Nov. 1985.*

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EFFECTS OF VARIATION IN FOOD INTAKE ON LOCOMOTORY PERFORMANCE OF JUVENILE GARTER SNAKES.—

Animals that ingest large masses of food should exhibit a decrease in locomotory performance (Taylor et al., 1980). Such reduced capabilities would be critical for the species if locomotion is important in their escape behavior. Many snakes feed on large prey yet still rely on locomotion in predator avoidance. Garter snakes of the genus *Thamnophis* often eat meals exceeding 30% of their body mass and use threat displays, biting and spraying musk as defense mechanisms (Fitch, 1965; pers. obs.); but escape also requires locomotion (Arnold and Bennett, 1984). Therefore, how locomotory performance is affected by successful foraging (i.e., a full stomach) is important to the overall fitness of these animals (Arnold, 1983).

Garland and Arnold (1983) found that endurance decreased with food intake in juvenile *Thamnophis elegans*. Distance moved by a snake prior to stationary defense was significantly less after the animal had ingested food of approximately 20% its body mass. Burst speed (time needed to move one meter) was not affected significantly by food intake. Results were similar when the lacertid lizard, *Eremias lugubris*, was force-fed termites (Huey et al., 1984; mean additional mass was 23%). In these lizards endurance decreased but sprint speed did not. These

authors did not test whether the decrease in locomotory performance was proportional to the mass of the meal. This could be critical for snakes for it may determine whether they should eat small frequent meals or infrequent but large prey. A simple way to answer this question is to test for correlation of the mass of prey eaten with the magnitude of decrease in performance (Garland and Arnold, 1983).

Materials and methods.—Subjects were laboratory-born, juvenile checkered garter snakes, *Thamnophis marcianus*, from four females captured near Los Angeles, La Salle Co., Texas. This species eats readily in captivity and juveniles will consume quantities up to and exceeding 50% of their body mass. The snakes were 10-12 wk old (body masses: 3.15-5.37 g, \bar{x} = 4.41, SD = 0.72; and snout-vent lengths: 21-25 cm, \bar{x} = 23.1, SD = 1.37) and were fed minnows (*Notropis* spp.) twice a week for several weeks prior to the experiment.

Locomotory performance was tested in a circular arena (diameter 90 cm; inside track circumference 384 cm) constructed of plywood with walls of aluminum flashing 15 cm high and an inside track width of 10 cm. The track was filled with corn-cob animal bedding to allow traction for the snakes. Trials were conducted under artificial light (L:D cycle 12:12) and at 25 C (\pm 2 C). This temperature is relevant since environmentally active *Thamnophis* have body temperatures of 25-28 C (Gregory, 1985). Each animal was tested under four conditions: after eating minnows weighing 10%, 30%, or 50% of their body masses and with an empty stomach (0%). Minnows were chosen that were within 2% of the mass required for the individual snake for a particular test. The order of test condition for each snake was randomized.

Each trial was performed 3-4 h after snakes were fed. The test animal was placed in the arena and chased vigorously around the track by tapping near its tail with a long-handled brush until the snake assumed a stationary defensive posture, or for a maximum of 2 min. Times to defensive response were recorded with a hand-held stopwatch. Distances were measured by multiplying the inside wall circumference by the number of times the snake circled the arena and adding any partial distance moved past the starting point. Snakes were tested every 4-6 d until each individual had completed tests under all four conditions. Individuals that did not eat on a particular day were offered food on subse-