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SELECTIVE PREDATION OF GRAY JAYS, *PERISOREUS CANADENSIS*, UPON BOREAL CHORUS FROGS, *PSEUDACRIS TRISERIATA*

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Wright (1948) pointed out that the conditions most favorable for rapid evolution exist when a species is divided into a large number of local populations, some of which are of small or medium effective size. Such conditions exist in the chorus frog, *Pseudacris triseriata,* in the mountains near Chambers Lake, Larimer County, Colorado. There are at least 21 breeding sites within a three mile radius among which exchange of individuals, and thus genetic interchange, occurs infrequently, if at all (Spencer, 1964).

Eight phenotypes of dorsal coloration occur, and three loci, each with two alleles, are involved (Matthews and Pettus, 1966). Tordoff et al. (1976) demonstrated significant differences among seven of these populations in the frequencies of alleles controlling dorsal coloration. Tordoff and Pettus (1977) further demonstrated that phenotypic frequencies for any one of three of these populations remained nearly constant over a five year period of study, and that the populations had small to medium sizes, ranging from 37 to 580 adults estimated from recapture data using a modified Lincoln index (Bailey, 1952). Matthews (1971) and Hess (1969), working in montane and piedmont populations of chorus frogs respectively, concluded that changes in gene frequencies during the life cycle appear to be cyclic. One allele of a pair increases in frequency during the aquatic phase, and the other allele increases during the terrestrial phase of the life cycle. However, there appears to be little or no change from generation to generation.

Tordoff and Pettus (1977) believed natural selection to be an important factor in maintaining the observed gene frequencies in these populations. Nevo (1973) drew similar conclusions for two other species of hylid frogs, *Acris crepitans* and *A. gryllus,* and suggested that visual selective predation was one factor involved in maintaining the color polymorphism.

In our montane populations, adults and recently metamorphosed young frogs are active during the day in mid and late summer and thus are susceptible to visual predation by diurnal predators. Gray jays, *Perisoreus canadensis,* are common in and around the meadows frequented by the frogs and they have been observed eating young frogs in these meadows.

Visual selection of prey by various bird species has been demonstrated previously under both laboratory and field conditions. Isely (1938) and Dice (1947), in laboratory situations, demonstrated that various species of birds strongly selected against prey which contrasted with the soil color. Kettlewell (1955, 1956, 1965) observed different species of birds prey upon moths under natural conditions. In the majority of the cases, the birds selected the moth which contrasted with the background coloration. Research on mimicry in Lepidoptera has added greatly to our knowledge of visual selection by various bird species (Ford, 1964; Terhune, 1977). Cain and Sheppard (1954, 1961), Cameron (1969), Parkin (1971), and others have shown that birds selectively feed on land snails (*Cepaea nemoralis, C. hortensis, Arianta arbustorum*), with intensity of selection on different morphs being highly correlated with the degree of crypticity.

The present study was undertaken to test, under laboratory conditions, whether gray jays would prey differentially on polymorphic chorus frogs exhibiting vary-

ing degrees of blending or contrasting with substrate coloration.

Materials and Methods

Although six different dorsal color phenotypes are commonly found in the Chambers Lake populations (Tordoff et al., 1976), only two, brown, and green-with-green-spots (henceforth referred to as green in this paper), were chosen for this study. These two are each unicolored and quite distinct in appearance.

Young frogs (15–20 mm snout–vent) which had recently metamorphosed were obtained as they emerged from breeding pools near Chambers Lake (elevation 3,100 m). The frogs were kept in terraria in a cold room until the tests were conducted.

Gray jays were captured in the vicinity of Chambers Lake using nylon mist nets. The birds were housed singly in hardware cloth cages with a perch in each cage. They were fed daily with canned dog food, mealworms, bird seed, and a mixture of ground apples, raisins, baby cereal, and liquid vitamins. The birds were allowed to eat ad lib. A dish of water placed in each cage was changed daily. The birds were not deprived of food prior to the selection tests.

The selection tests were conducted in a room 7 × 10 ft, and 8 ft high. The window and built-in bookcase were covered with roofing paper to prevent any orientation to light or extra perches, respectively. The floor was divided into two 5 × 7 ft halves with an 8 in high center divider. An aluminum strip was placed along the top of the divider and around the perimeter of the room at a height of 8 in. It was curled over like an awning to prevent frogs from climbing the walls or from moving from one side of the room to the other.

Terrycloth, dyed green or brown, was used as a substrate for the two halves of the room. This provided a background which was similar to each of the two color phenotypes studied.

Two perches were constructed of 6 ft, 2 × 4 in lumber with four 12 in dowels placed perpendicular to the 2 × 4's at 1 ft intervals from 2 to 5 ft above the ground. A piece of ¼ in plywood 1 ft^2 was fastened to the top of each perch and a bowl of water was placed on each of them to allow the bird access to drinking water. One perch was placed in the center of each side of the room. Lighting was provided by two 100 watt incandescent bulbs in ceiling sockets, one over each perch.

A window between the test room and an adjoining room allowed observation of the test without disturbing the bird or the frogs. The window was covered with brown paper with the exception of small slits which allowed the researcher to observe the tests but prevented movement in the other room from being detected by the bird.

Since the test room was of limited area, only a small number of frogs could be used in a single test. Each test utilized 40 frogs. Ten brown and ten green frogs were placed on each side of the room and allowed one-half hour to become accustomed to the room. A bird was then placed in the room and left until it had consumed one-half of the frogs from at least one side of the room at which time it was removed from the room. The remaining frogs were then recovered and their colors determined.

The selection test data were subjected to Chi-square analyses based on the null hypothesis of no difference in the number of each phenotype eaten on a side to determine if the birds selected prey according to the blending or contrasting of the prey color with substrate color.

Since the birds were allowed to capture a set number of frogs before the test was stopped, the ratio of green to brown prey was not always 1:1. The frequency changed as each frog was captured. Thus, the appropriate Chi-square test compares frequency eaten with frequency presented at the start using the hypergeometric variance (O'Donald and Pilecki, 1970; Manly et al., 1972). The formula employed is: $\chi^2 = (r'N - RY)^2(N - 1)/(RBYZ)$ with one degree of freedom, where r' is the number of contrasting frogs eaten, N is the total number of frogs presented, Y is the total

TABLE 1. *Results of selection tests involving gray jays.*

Bird number	No. of tests	Total no. of frogs eaten	Brown side				Green side			
			No. of green frogs eaten	No. of brown frogs eaten	Total eaten	Chi-square value	No. of green frogs eaten	No. of brown frogs eaten	Total eaten	Chi-square value
1969-1	4	39	10	2	12	6.20*	13	14	27	.06
1969-2	4	62	21	16	37	1.24	10	15	25	1.44
1969-3	3	58	16	15	31	.07	14	13	27	.07
1969-4	3	75	15	19	34	1.07	18	23	41	1.89
1970-1	3	54	16	11	27	1.66	11	16	27	1.66
1970-2	3	60	18	14	32	1.05	11	17	28	2.37
1970-3	4	71	24	10	34	9.90**	19	18	37	.05
1970-4	3	63	16	12	28	1.05	15	20	35	1.69
Totals	27	482	136	99	235	10.30**	111	136	247	4.66*
G (heterogeneity)[1]					9.09				2.15	
Degrees of freedom					7				7	

[1] Compared to Chi-square distribution.
* Chi-square test significant at 0.05 level with 1 *d.f.*
** Chi-square test significant at 0.01 level with 1 *d.f.*

number of frogs eaten, R is the number of contrasting frogs presented, B is the number of blending frogs presented, and Z is the total number of frogs not eaten ($N - Y$) (Manly et al., 1972, p. 729).

In order to determine if this Chi-square test may also be employed on the data for all birds on one color substrate combined, a G test for heterogeneity was carried out (Sokal and Rohlf, 1969).

RESULTS AND DISCUSSION

The results of the selection tests along with the Chi-square analyses of these data are presented in Table 1. Each bird was employed in three or four tests. The length of time required for a bird to complete a test ranged from 45 min to 8 h. The results of all tests with a single bird are combined in these tables. In all but three of the 16 test cells (a test cell is the combined results of one bird on either the green or the brown background) there is a tendency for the frogs contrasting with the background coloration to have a selective disadvantage compared to the cryptically colored frogs. The mean selective disadvantage is 25% for the green frogs on the brown background and 17% for brown frogs on the green background. The Chi-square tests in two of the 16 test cells (1969-1 [.05 level], and 1970-3 [.01 level], both on the brown side) are significant. Although none of the other individual Chi-square values is significant, the combined Chi-square value for the brown side (10.30) is significant at the .01 level, and the Chi-square value for the combined results on the green side (4.66) is significant at the .05 level. The G tests indicate that there is homogeneity among the birds for a side and therefore the results for individual birds may be combined for analysis.

These selection tests indicate that gray jays may prey selectively on boreal chorus frogs. The hunting behavior of the jays may account for this differential predation. Humans hunting for frogs in these meadows walk slowly through the meadows and rely on the frogs' movements as they are flushed to locate them. Comparisons of phenotypes of frogs caught in this manner with phenotypes of frogs caught in pitfall traps revealed no bias toward any phenotype (Spencer, 1964). The jays, however, do not rely on making the frog move in order to locate it. The majority of the time that a jay was in the test room was spent on one of the two perches. When a bird became interested in feeding, it would sit on one of the rungs of a perch,

watch the ground, and then it would fly either directly to the ground or to the center divider, then immediately to the ground, and capture a frog. In most of the cases the bird would pick up a frog without hopping along the ground. It would then take the frog to the perch, eat it, and then repeat the hunting sequence. This type of behavior has been observed in nature. The flights of the jays to the ground from perches ranged from one to over 100 ft from heights of from one to 20 ft, although more than 75% were of less than 10 ft from heights of less than 5 ft.

Although the above behavior indicates that gray jays may locate frogs without actively flushing them, if the frog moves prior to the jay leaving the perch, and if it is this movement which attracts the jay, the most important visual clue for the jay may be the motion and not the frog's color. It was not possible to determine if motion was an important clue by watching the jays near Chambers Lake because the frogs were always shielded from my view by ground vegetation. However, in 30 instances of observing the jays in the test room, it appears that the frog need not move in order for the jay to notice it on an artificial background. Although there may have been slight movements by the frog, such as the throat moving during breathing, in the few minutes preceding its capture by the jay, I did not detect any movements of the frogs. It thus appears that the jays can perceive and capture frogs without the jays first being attracted by movement.

While these tests demonstrate that gray jays can selectively prey upon frogs according to substrate color and phenotypic coloration, this does not prove that such selection accounts for all or even part of the observed phenotypic frequency differences reported for these frog populations (Tordoff et al., 1976; Tordoff and Pettus, 1977). Preliminary attempts to quantify local substrate coloration and correlate it with phenotypic frequencies indicate that a correlation may exist, but insufficient data are available to make any conclusive reports.

Summary

Laboratory tests demonstrated that gray jays, *Perisoreus canadensis,* prey selectively upon boreal chorus frogs, *Pseudacris triseriata,* according to whether the frog's dorsal color contrasts or blends with the substrate color. The hunting behavior of the jays is postulated to account for this. Gray jays are thus suspected of being an important selective agent in maintaining differences in dorsal coloration phenotypic frequences in montane populations of the chorus frogs.

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Literature Cited

Bailey, N. T. J. 1952. Improvements in the interpretation of recapture data. J. Anim. Ecol. 21:120–127.

Cain, A. J., and P. M. Sheppard. 1954. Natural selection in *Cepaea.* Genetics 39:80–116.

———. 1961. Visual and physiological selection in *Cepaea.* Amer. Natur. 95:61–64.

Cameron, R. A. D. 1969. Predation by song thrushes *Turdus ericetorum* (Turton) on the snails *Cepaea hortensis* and *Arianta arbustorum* (L.), near Rickmansworth. J. Anim. Ecol. 38:547–553.

Dice, L. R. 1947. Effectiveness of selection by owls of deer-mice (*Peromyscus maniculatus*) which contrast in color with their background. Contr. Lab. Vert. Biol. Univ. Mich. No. 34:1–20.

Ford, E. B. 1964. Ecological Genetics. Methuen, London.

Hess, J. 1969. Changes in frequency of the green-spot phenotype in piedmont populations of the chorus frog. Ph.D. Dissertation. Colorado State Univ., Fort Collins.

Isely, F. B. 1938. Survival values of acridian protective coloration. Ecology 19:370–389.

Kettlewell, H. B. D. 1955. Selection experiments on industrial melanism in the Lepidoptera. Heredity 9:323–342.

———. 1956. Further selection experiments on industrial melanism in the Lepidoptera. Heredity 10:287–303.

———. 1965. Insect survival and selection for pattern. Science 148:1290–1296.

MANLY, B. F. J., P. MILLER, AND L. M. COOK. 1972. Analysis of a selective predation experiment. Amer. Natur. 106:719–736.

MATTHEWS, T. C. 1971. Genetic changes in a population of boreal chorus frogs (*Pseudacris triseriata*) polymorphic for color. Amer. Midl. Natur. 85:208–221.

MATTHEWS, T. C., AND D. PETTUS. 1966. Color inheritance in *Pseudacris triseriata*. Herpetologica 22:269–275.

NEVO, E. 1973. Adaptive color polymorphism in cricket frogs. Evolution 27:353–367.

O'DONALD, P., AND C. PILECKI. 1970. Polymorphic mimicry and natural selection. Evolution 24:395–401.

PARKIN, D. T. 1971. Visual selection in the land snail *Arianta arbustorum* (L.). Heredity 26:35–47.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco.

SPENCER, A. W. 1964. The relationship of dispersal and migration to gene flow in the boreal chorus frog. Ph.D. Dissertation. Colorado State Univ., Fort Collins.

TERHUNE, E. C. 1977. Components of a visual stimulus used by scrub jays to discriminate a Batesian model. Amer. Natur. 111:435–451.

TORDOFF, W. III, AND D. PETTUS. 1977. Temporal stability of phenotypic frequencies in *Pseudacris triseriata* (Amphibia, Anura, Hylidae). J. Herp. 11:161–168.

TORDOFF, W. III, D. PETTUS, AND T. C. MATTHEWS. 1976. Microgeographic variation in gene frequencies in *Pseudacris triseriata* (Amphibia, Anura, Hylidae). J. Herp. 10:35–40.

WRIGHT, S. 1948. On the roles of directed and random changes in gene frequency in the genetics of populations. Evolution 2:279–294.

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