DIFFERENTIAL PERCH SITE SELECTION BY COLOR MORPHS OF THE RED-TAILED HAWK (*BUTEO JAMAICENSIS*)

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ABSTRACT.—Ecological relationships among color morphs of the Red-tailed Hawk (*Buteo jamaicensis*) were studied during two successive winters in Benton County, Arkansas. Each mature hawk observed was assigned to one of three predetermined plumage categories (light, intermediate, dark) on the basis of ventral pigmentation. Multivariate analysis of variance showed a significant difference between light and dark morphs in perch site selection. A perch site openness gradient was established using discriminant function analysis. Light hawks occupied open perch sites, while dark hawks more frequently occupied perch sites characterized by dense stem cover. I suggest that the morphs were associated with perch sites that best concealed them from prey.
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THE Red-tailed Hawk is a polytypic species in which at least one subspecies (*Buteo jamaicensis calurus*) exhibits color polymorphism (Taverner 1936, Bent 1937). Paulson (1973) has suggested that the polymorphism exhibited by many avian predators, including the Red-tailed Hawk, is maintained by apostatic selection. In apostatic selection, the morphs that stand out from the norm would have a selective advantage by virtue of their rarity (Clarke 1962, 1969). Inherent in this hypothesis is the assumption that prey of a polymorphic predator are capable of forming a specific "avoidance image" for the common color morph of that predator. There is yet no conclusive experimental evidence to support this assumption. Furthermore, intuitively it would seem maladaptive for an organism to form such a specific "avoidance image" based on pigmentation alone and to ignore all slightly different, less common color morphs of a predator. Arnason (1978) has pointed out that, although recognition of a predator morph may be learned rather than fixed, providing for the flexibility to deal with changing situations, learning presents a problem to the apostatic selection hypothesis because the prey get eaten. Arnason also pointed out that a prey individual may encounter only one of the color morphs of a territorial predator. Thus, there are at least three major obstacles to applying the apostatic selection hypothesis to predators such as the Red-tailed Hawk.

Many authors, including Levene (1953), Van Valen (1965), Levins and MacArthur (1966), and Hedrick et al. (1976), have suggested that environmental factors may play a role in the maintenance of polymorphism in a population, each of the morphs being best adapted to, and therefore associated with, a slightly different subunit of the environment. There are few reported examples of ecological differences between color morphs of a polymorphic bird species. Johnson and Brush (1972), however, have reported marked ecological differences between presumed color morphs of the Sooty-capped Bush-Tanager (*Chlorospingus pileatus*). Murton (1971) suggested that differences in behavior and ecology existed between color morphs of several Ardeids, but his observations lacked quantitative analysis.

Although color polymorphism in the Red-tailed Hawk has been discussed by several authors (e.g. Taverner 1927, 1936, Bent 1937, Huxley 1955, Paulson 1973), no information regarding the comparative ecology of the color morphs is available.

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The large and phenotypically diverse assemblage of Red-tailed Hawks that overwinters in northwestern Arkansas provides an excellent opportunity for study. The purpose of this project was to determine whether significant ecological differences existed among color morphs of the Red-tailed Hawk during their winter residence in northwestern Arkansas.

MORPH VARIATION

I examined study skins from the University of Kansas Museum of Natural History and the University of Arkansas Museum to appraise the potential range in plumage variation among Red-tailed Hawks overwintering in northwestern Arkansas. A graded series of nine variants showing increasingly darker plumage was established, against which all specimens were matched. With experience it was easy to assign specimens to appropriate categories. Subspecific designations were disregarded, and immature birds were eliminated from the study. The following descriptions refer only to those characters used in assigning a specimen to one of the categories; other variation is omitted (numerals I–IX refer to each of the nine variants arranged in order of increasingly darker plumage, and parenthetical numbers indicate how many specimens were assigned to each category).

I. (4) Thin, incomplete brown band across jugulum; gular region white. Breast white, with a few dark specks along sides and flanks. Incomplete brown band extending from flanks across abdomen. Shanks white with scattered dark specks. Overall appearance of underparts white. Example: KU24751 (catalog number of specimen from University of Kansas Museum of Natural History).

II. (15) Plumage pattern similar to variant I, but overall appearance of underparts cream rather than white. Example: KU17131.

III. (6) Throat and breast light rust with widely scattered brown specks along sides and flanks. Abdomen light rust with few specks. Example: KU20610.

IV. (5) Throat lightly speckled with brown. Breast cream with scattered brown specks. Flanks heavily speckled with brown extending across abdomen to form thin, complete band. Shanks cream with scattered brown specks. Example: KU9590.

V. (5) Throat and upper breast heavily speckled with brown on rusty background. Abdomen and shanks heavily speckled with brown on cream background. Example: KU13634.

VI. (4) Solid brown band across jugulum. Gular region and shanks rust with dark specks. Abdomen dark brown. Example: KU4309.

VII. (9) Underparts uniformly black with scattered white specks. Example: KU17129.

VIII. (7) Throat, breast and shanks deep rust; abdomen black. Example: KU18543.

IX. (6) Underparts uniformly black. Example: KU18478.

Not all of the characters used here to categorize the nine variants are easily discerned in the field. There are marked discontinuities, however, between variants III and IV, and between variants VI and VII. Therefore, each hawk observed in the field was classified only as light (I–III above), intermediate (IV–VI above), or dark (VII–IX above).

STUDY AREA AND METHODS

The study was conducted in a 244-km^2 area near Centerton, Benton County, Arkansas. The region, varying from flat terrain to abrupt ridges, was covered mostly by alternating pastureland and oak-hickory forest, with some old fields, plowed cropland, and winter stubble fields.

During the study, I recorded data from 75 perched hawks (25 per morph group) and 45 soaring hawks (15 per morph group). Observations were made between 14 December 1976 and 25 February 1977 and between 2 November 1977 and 28 January 1978. I attempted to collect the data under a wide range of weather conditions. Although I did not knowingly collect data on any individual hawk more than once, it is probable that some individuals were used more than once during the study. The data were collected as I drove along section roads throughout the study area for an average of 120 km per observation day. Ambient temperature and relative humidity were measured every hour with a sling psychrometer. The remainder of the data were recorded at the time of the hawk sighting. I classified each hawk as light, intermediate, or dark with the aid of a 20× spotting scope. The classification of some soaring hawks was difficult under certain lighting conditions and was accomplished only after lengthy observation. A Dwyer wind meter was used to measure wind velocity. Solar illumination was measured in foot candles with an illuminometer. Percentage cloud cover was obtained with a circular mirror, 15 cm in diameter, marked

TABLE 1. Coefficients of correlation between measured perch site and habitat variables and the first two discriminant functions.

Habitat and perch site variables	DF I	DF II
Percentage forest	0.253	−0.190
Percentage cropland	−0.036	0.735
Percentage pasture	−0.190	0.514
Percentage old field	−0.068	0.005
Percentage stem cover surrounding hawk	0.801	0.272
Height of perch (tree, utility pole, etc.)	0.160	−0.225
Distance between the hawk and the top of the perch	0.711	−0.061

with a 25-unit grid. I held the mirror at chest height and kept it tilted at a 20° angle to the ground to reflect the sky directly above and slightly in front of me. Readings were taken in four orthogonal compass directions. The initial direction was set by the random position of the crosshairs of a sighting tube. Percentage cloud cover equalled the total number of grid units containing cloud reflections. This technique was developed from the suggestions of D. James (pers. comm.).

Each hawk that was perched when first observed was considered the center of a circular 0.081-ha sample area. Four orthogonal transects were established from the center of each area, the first being set by the random position of the crosshairs of a sighting tube. Each transect was 22.5 m long and constituted the radius of the 0.081-ha circle. The habitat category (forest, cropland, pasture, or old field) was recorded at each of 15 randomly generated points along each of the four transects. Thus, there was a total of 60 points used for calculating habitat percentage values for each perched hawk. This sampling procedure is a modification of one described in detail by James and Shugart (1970). A clinometer was used to measure the height of the perch (tree, utility pole, etc.) and the height of the hawk's perch site. The perch site refers to the actual location of the perched hawk. From these measurements I determined the distance between the hawk and the top of the perch. The percentage stem cover surrounding each hawk was estimated with a pane of transparent glass marked with a 100-unit grid. From a kneeling position 20 m from the perch, I held the device at arm's length and placed the hawk's perch site in the center of the grid. Percentage stem cover equalled the number of grid units containing stems. This procedure was repeated from each of the four transects surrounding the perch, and the four resultant percentages were averaged for each hawk.

Habitat values were obtained for each soaring hawk in generally the same manner as for perched hawks. The approximate spot over which the bird was first observed soaring was considered the center of a circular 0.162-ha sample site. Each of the four transects was 45 m long and percentages were calculated from 25 random points along each transect, or a total of 100 points. Soaring altitude was estimated by a technique suggested by D. James (pers. comm.). A transparent pane of glass was marked with four silhouettes of decreasing size, representing Red-tailed Hawks as they would appear at 23-m distance intervals up to 92 m. A taxidermy specimen was used to calibrate the scale. Altitude measured in this way must be considered as only a rough estimate due to the variation in size among individual hawks. Hawks soaring at altitudes greater than 92 m were grouped into one altitude category.

The data were analyzed using an IBM-370 Model 155 digital computer and statistical programs in the computer library at the University of Arkansas. Soaring data and perching data were analyzed separately. In order to meet the normality assumptions of certain statistical procedures used, all of the percentage values were adjusted using the angular transformation discussed by Sokal and Rohlf (1969). Also, 1.0 was added to all measurements of some factors to eliminate null matrices.

Box's test (Sokal and Rohlf 1969) indicated that the variance of the perch site variables was not homogeneous among the three morph groups. Because the validity of some of the statistical procedures used demands at least approximate covariance homogeneity among experimental groups, an attempt was made to stabilize the variance by using an iterative procedure that generates a power transformation for each variable. These procedures were patterned after Box and Cox (1967) and Andrews et al. (1971). Although complete stabilization was not attained, the F statistic for 56 and 14,807 degrees of freedom was reduced from 3.09 with untransformed data to 1.72 with transformed data, which is the best that can be attained with power transformations on these three groups with seven variables each.

Multivariate analysis of variance (Morrison 1967, Cooley and Lohnes 1971) with a step-down procedure (Bargmann 1962) was used to test for a significant difference among the morph groups with respect to either soaring activity or perch site selection and to identify any variables contributing significantly to

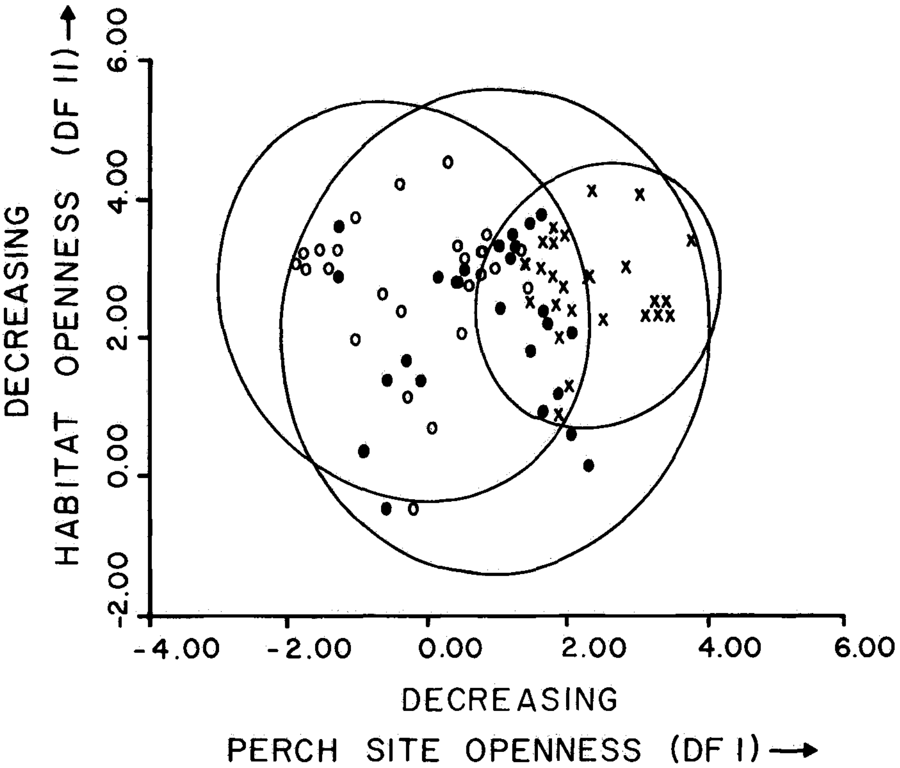

Fig. 1. Ordination of the morph groups' perching niches with 95% confidence ellipses based on discriminant function analysis (O = light morphs, × = dark morphs, ● = intermediate morphs).

the difference. Discriminant function analysis (Fisher 1936, 1938) was used to maximize any differences among the groups. See Green (1971) for a discussion of discriminant function analysis as applied to ecological data.

RESULTS

Although multivariate analysis of variance showed no significant differences among the three morph groups in soaring activity, it showed a highly significant difference among the groups in perch site selection ($-\text{m} \ln \lambda = 60.727$, $P < 0.001$). The step-down procedure showed that the distance between the hawk and the top of the perch ($P < 0.001$) and the percentage stem cover surrounding the hawk ($P < 0.05$) contributed significantly to the difference. Paired comparisons were made to determine which morph groups exhibited consistent differences in perch site selection. Neither light nor dark morphs differed significantly from intermediate morphs ($P > 0.05$), but there was a highly significant difference between light and dark morphs ($-\text{m} \ln \lambda = 57.46$, $P < 0.001$).

The discriminant function values combine the properties of variation exhibited by all perch site variables adjusted so that the effects of the variation are maximized with respect to separating the morph groups. The percentage stem cover surrounding the hawk and the distance between the hawk and the top of the perch were highly correlated with the first discriminant function, DF I (Table 1). DF I describes a variation among the morphs with respect to perch site openness. Low values associated with DF I indicate the use of perch sites located near the top of the perch, surrounded by few stems. The DF I mean score for the light group is −0.389, for the intermediate group 0.893, and for the dark group 2.300. The light hawks used perch sites that were relatively open, and dark morphs used perch sites characterized by dense stem cover.

There is very little difference among the morphs with respect to DF II. Percentage pasture and percentage cropland have the highest positive correlations with DF II, while perch height and percentage forest have the highest negative correlations (Table 1). DF II is interpreted to represent habitat openness surrounding the perch. The DF II mean scores for the light, intermediate, and dark morphs are 0.025, 0.021, and 0.026, respectively. Thus, all of the morphs occupied the same habitat (defined by DF II) but selected different perch sites (defined by DF I) within the habitat.

The discriminant functions provide axes for a two-dimensional ordination of the morph groups (Fig. 1). The available perching niche may be defined here as the space, relative to the discriminant function axes, within which all observations recorded during this study lie (see Green 1971). Relative niche breadths (Green 1974) are shown by 95% confidence ellipses drawn about the morph groups. Figure 1 shows that the intermediate morphs, though not using either extreme of the perch site openness gradient, occupied a wider range of perch sites than did the other morphs. The dark morph group exhibited the least variability in perch site selection.

DISCUSSION

The results suggest that light morphs may be disadvantaged if perched in sites characterized by dense stem cover, and dark morphs may be disadvantaged if perched in relatively open sites. Further studies are needed to actually test this hypothesis, however. Possible factors responsible for the differential perch site selection are discussed below.

Thermoregulation.—Hamilton and Heppner (1967) presented evidence that dark plumage decreased energy requirements in cold ambient temperatures (below lower critical) by absorbing more solar energy than light plumage. But if ambient temperature exceeds the upper critical, dark birds exposed to solar radiation may incur an excessive heat load. Heppner (1970) suggested that light-colored birds receive less advantage from the sun in cold weather than do dark birds but do not heat up as quickly as dark birds in hot weather. Therefore, dark hawks might require shady perch sites under the same conditions that light hawks could use more open perch sites. I found no association between weather conditions and perch site selection, however, for any morph group. Walsberg et al. (1978) recently showed that dark birds exposed to solar radiation in the presence of moderate wind velocities could avoid an excessive heat load by ruffling the plumage. Furthermore, there is little variation among the morphs' dorsal pigmentation, and much of the solar radiation would presumably be absorbed directly by the dorsal surface. As more information becomes available, the importance of thermoregulation to differential perch site selection by the morphs can be better evaluated.

Crypsis.—Several authors (e.g. Kettlewell 1956, Murton 1971, Johnson and Brush 1972, Otte and Williams 1972) have associated color polymorphism with crypsis in heterogeneous environments. Color polymorphism in the Red-tailed Hawk is expressed ventrally, on the surface most exposed to prey. Dense stem cover provides a dark background against which light hawks are more visible than dark hawks to the human observer. Conversely, the absence of cover provides a relatively light background against which dark hawks are more conspicuous. Phillips (1962) showed that by daylight in open situations white plumage allowed the adults of some piscivorous Larids to get closer to potential prey before the prey took avoidance action. Inasmuch as most hunting by Red-tailed Hawks is done from a perch (Fitch et al. 1946), it would seem advantageous for a perched hawk to be concealed from potential prey, assuming that the prey are able to locate and avoid noncryptic hawks and thus act as selective agents. Sufficient information regarding the ability of prey to locate perched hawks is not yet available. The Red-tailed Hawk's diet can be very diverse (Craighead and Craighead 1956), and it would be difficult to determine how great a proportion of the total diet that discriminating prey must comprise in order to exert a significant selective pressure (Paulson 1973). The apparent flexibility in perch site selection exhibited by the intermediate morphs (Fig. 1) indicates that virtually all sites within the available perching niche are equally good for hunting, barring the effects of polymorphism. Future studies are needed to determine the success of representatives of each morph group when hunting from various types of perches.

It is not known whether the differential perch site selection observed in this study is an extension of habitat utilization on the breeding grounds or is unique to these wintering grounds. Because starvation outside of the breeding season may be a critical factor in limiting wild bird populations (Lack 1966), any selective pressures associated with perch site utilization may be particularly strong in winter. Fretwell (1972) pointed out that the feeding behavior of birds may differ greatly from season to season and geographic region to region. *Buteo j. calurus* is evidently the most variable subspecies of the Red-tailed Hawk in plumage pigmentation (Taverner 1936). This race inhabits a strikingly heterogeneous environment across its range, breeding from saguaro-palo verde desert to boreal forest. Color polymorphism may allow *B. j. calurus* to broaden and partition its overall ecological niche, thus relaxing intraspecific competition. A comparison of habitat utilization among color morphs of this subspecies during the breeding season should prove helpful in assessing the role that ecological factors may play in maintaining the polymorphism.

Mayr (1963) and Jones et al. (1977) have pointed out that many types of environmental and genetic factors may act to maintain polymorphism in a population, and that their relative importance varies between populations or loci. Pleiotropy may be involved in the polymorphism exhibited by the Red-tailed Hawk, whereby color determines only a part of the selective value of a genotype. Polymorphism may be tolerated in the population because the phenotypes are selectively neutral. Information regarding the genetic basis of color polymorphism in the genus *Buteo* is vital to an understanding of the processes responsible for the maintenance of plumage variation exhibited by the Red-tailed Hawk.

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