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RAPTOR MORTALITY DUE TO DROWNING IN A LIVESTOCK WATERING TANK

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On 9 July, 1974 in Oneida County, S.E. Idaho, we discovered the partially decomposed remains of seven American Kestrels (*Falco sparverius*), and two unidentified passerines at the bottom of an empty livestock watering tank. The tank was circular, 4.9 m in diameter, 0.5 m deep and constructed of corrugated steel with a cement bottom. We assumed that the birds drowned after entering the tank for unknown reasons.

Two similar tanks in other parts of the region were later investigated and found to contain small avian remains in one, while a White-footed Deer Mouse (*Peromyscus maniculatus*) and Western Meadowlark (*Sturnella neglecta*) were in the other. Portions of Black-tailed Jackrabbits (*Lepus californicus*) were found in both of these tanks, their condition suggesting that they had been eaten by raptors. In addition, we found castings of Burrowing Owls (*Speotyto cunicularia*) at two of the three watering tanks.

Anderson (*Auk* 81:332-352, 1964) noted that a Prairie Falcon (*Falco mexicanus*) drowned in a stock tank. The bird was an adult female, nesting approximately 500 m from the stock tank in which it died, in the spring of 1961 (Anderson, pers. comm.). We have found no other references to this type of mortality in the literature. Our observations extend Anderson's record to another species of raptor and

suggest that additional raptor species as well as smaller bird and mammal species may suffer similar deaths.

Perhaps raptors enter stock tanks for any of several reasons. Tanks may serve as a perch, as is evidenced by the presence of probable prey remains and castings in them. The raptor may enter the water to retrieve dropped prey items and then be unable to extricate itself. The water itself may be an attraction to the raptor. Lastly, and perhaps most logically, the raptor may be drawn to the tank by the presence of potential prey species which themselves have been attracted and trapped by the water. Thrashing movements of a trapped and drowning animal probably would trigger intense investigative and hunting behavior by raptors as well as other predators. Young inexperienced raptors, newly fledged from nests near stock tanks would be most vulnerable.

During the spring, summer, and fall when livestock are pastured in the vicinity, the tanks usually contain water. One rancher stated that he drained his tanks when they were not in use to prevent hawks from drowning in them, an occurrence he had seen several times (Elison, pers. comm.).

Drowning in livestock watering tanks may be significant due to the widespread use of such tanks throughout the arid and semi-arid western United States. This cause of death could be reduced simply by floating a large block of wood in the tank; this could facilitate escape from the water for trapped animals.

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THE EVOLUTION OF COLOR DIFFERENCES BETWEEN NASHVILLE AND VIRGINIA'S WARBLERS

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Within the parulid genus *Vermivora*, the Nashville Warbler (*V. ruficapilla*) and Virginia's Warbler (*V. virginiae*) are closely related (Griscom and Sprunt

1957, Mengel 1964, Lowery and Monroe 1968, Stein 1968). Mayr and Short (1970) regarded the two forms, plus the Colima Warbler (*V. crissalis*), as component species of a superspecies, while Phillips et al. (1964) treated all three as conspecific, based on vocalizations and behavior. Although standard references (e.g., A.O.U. 1957) imply that *V. ruficapilla* and *virginiae* are locally sympatric during the breeding season in northern Utah and southern Idaho, and therefore have proved their biologic species status, a review of verifiable breeding distributional records demonstrates that the two forms are strongly allopatric (Johnson 1976). Thus, continued main-

tenance of these warblers as species rests largely on inferences drawn from differences in appearance. The Nashville Warbler is richly yellow over the entire underparts; the Virginia's Warbler, in contrast, is whitish-gray on the underparts except for two pale yellowish patches, variable in size, one on the upper breast and the other on the under tail coverts. Dorsally, the species are identical with a gray forehead, nape, and auriculars, chestnut crown patch, and white eye ring, but differ in the color of the back and scapulars, which are olive-green in the Nashville Warbler and gray in the Virginia's Warbler, and in the color of the rump, which is yellowish-green in the former species and greenish-yellow in the latter species.

The major differences in appearance between these two warblers have not previously been investigated in detail. In this paper we report the analyses of carotenoid feather pigments of the breast and rump, and speculate on the events that led to the evolution of the color differences between the two species. Identity and distribution of feather carotenoids are relevant to the problem of the systematic relationship of the Nashville and Virginia's warblers and to the broader question of the adaptive evolution of color differences among closely-related birds (Brush and Power 1976).

MATERIALS AND METHODS

Breast and rump feathers were analyzed from four specimens each of *Vermivora r. ruficapilla*, *V. r. ridgwayi* and *V. virginiae* from the Museum of Vertebrate Zoology. The techniques for preparation, identification, and analysis of the feather pigments in these 12 specimens were essentially those described by Johnson and Brush (1972) and Brush and Seifried (1968). Pigments from samples were extracted from pre-weighed feathers in alkaline ethanol on a steam bath. The material was transferred to hexane for subsequent analysis.

RESULTS

Chemical and spectral analysis and co-chromatography with purified known samples identified the carotenoid pigment in the feathers from the breast and rump of all three taxa as lutein (3,3'-dihydroxy- α -carotene). No other carotenoid pigment was detected. Only a single spot was present in thin-layer chromatography in a variety of solvent systems. The pigment has complex visible spectra with peaks at 424, 446 and 474 nM in hexane and at 425, 448 and 477 nM in ethanol. Both the spectra and the mobility on TLC agree with those from lutein. The partitioning coefficient was 19:81 in 95% methanol and 47:53 in 85% methanol. These values are in agreement with those published for lutein. Lutein is also known to be present in other species of warblers and is probably widely distributed in passerine birds.

The quantity of pigment deposited in the breast and rump plumage varied according to the area and differed among taxa (table 1). The rump patches of all three taxa were similar in pigment content and were consistently more intensely pigmented than the breast in the same individual. The two subspecies of Nashville Warbler had concentrations of pigment in the breast plumage which were double that of *V. virginiae* ($P < 0.001$; t-test).

TABLE 1. Carotenoid pigment concentration (as mg/100 gm feathers) of breast and rump plumage in three closely-related taxa of warblers.

	M.V.Z. Specimen Number	Breast	Rump
<i>Vermivora</i>			
<i>ruficapilla</i>			
	107514	39.54	55.17
	127879	48.70	54.52
	127883	51.90	72.69
	127886	38.90	42.19
Mean		44.70	56.10
<i>Vermivora</i>			
<i>ruficapilla</i>			
	116943	40.20	49.97
	116944	42.80	—
	116945	50.45	36.34
	116946	22.29	44.78
Mean		38.90	43.60
<i>Vermivora</i>			
<i>virginiae</i>			
	67478	19.50	33.75
	112974	23.60	72.69
	9991	23.40	25.31
	64997	16.81	67.49
Mean		20.80	49.70

DISCUSSION

Biochemical origin of color differences. Lutein concentration provides the basis for the color differences in the breast plumage of the Nashville and Virginia's warblers. The difference is apparently one of simple dilution in the paler species. This is not unprecedented among birds and probably represents the simplest possible control mechanism for the modification of plumage color in closely-related forms (Johnson and Brush 1972). The differences in the species considered are chemically (and probably genetically) simple yet have obvious biological importance.

Color differences in closely-related birds may be caused by a variety of biochemical mechanisms with different genetic controls (see Brush and Power 1976, for summary). In every case the differences appear to be under strong selection pressure because of the crucial role of plumage color and pattern in mate selection, species recognition and in general interactions between individuals. Birds are highly visual animals and the physical causes of plumage color differences thus have evolutionary significance.

The evolution of interspecific differences in plumage coloration. The strongly allopatric nesting environments of these two species of warblers differ greatly in climate, vegetation, flora, and in background color (Johnson 1976, Baldwin 1973). The plumage color of these warblers corresponds broadly to the general color of their preferred nesting habitats. Nashville Warblers are predominantly green and bright yellow whereas Virginia's Warblers are mainly gray with limited patches of pale yellow. The striking difference in appearance of plumage between the two species apparently was accomplished solely through a reduction in lutein pigmentation, thereby exposing underlying grayish melanins in the Virginia's Warbler. This simple mechanism, that achieves pronounced visual effects, was demonstrated in the Sooty-capped Bush Tanager (*Chloro-*

spingus pileatus) by Johnson and Brush (1972). A selection pressure sufficient to encourage reduction of yellows and exposure of grays in plumage could operate through background matching that results in lessened predation. Other examples exist, in species with coastal and interior forms, in which the subspecies of the Great Basin and Rocky Mountains are grayer than those along the coast. These include the Scrub Jay (*Aphelocoma coerulescens*), Plain Titmouse (*Parus inornatus*), Bush-tit (*Psaltriparus minimus*) and Solitary Vireo (*Vireo solitarius*). The warblers represent an extreme manifestation of a general trend seen commonly at the subspecific level of differentiation in this region of western North America. Other species of warblers illustrate the same phenomenon. For example, the Black-throated Gray Warbler (*Dendroica nigrescens*), which Mengel (1964: 20) noted was "nearly devoid of xanthic pigments," is most abundant in the pinyon-juniper zone of the Great Basin, although it occurs locally and in reduced numbers all the way to the Pacific Coast. Its closest relatives, the Townsend's Warbler (*Dendroica townsendi*) and Hermit Warbler (*D. occidentalis*), both richly endowed with carotenoid pigments, have more coastal distributional centers, comparable to that of the western subspecies of the Nashville Warbler.

Plumage color and reproductive isolating mechanisms. Because of distinctive preferences in nesting habitats it is unlikely that breeding Nashville and Virginia's warblers meet in numbers at some presently undiscovered site (Johnson 1976). But given the remote possibility of local interspecific contact during the breeding season, subtle differences in vocal and display behavior, interacting in complex ways with strong differences in plumage color pattern, could easily serve as reproductive isolating mechanisms between individuals in immediate association.

Two additional points of interest to evolutionists emerge from our data. These warblers probably have never been sympatric. They have evolved so recently from a common ancestor that their current distributions reveal the basic allopatry of the speciation process, and their treatment by Mayr and Short (1970) as component species of a super-species supports this view. Further, it is a correlate of our argument that the differences in habitat preference and plumage color are adaptations evolved in response to selective pressures of the respective environments presently inhabited. Specific characters (e.g., plumage color patterns) that evolved in relation to one adaptation (background matching) may have the potential to serve a new adaptive function (reproductive isolation), a clear example of "pre-adaptation" as defined by Bock (1959). These points also relate to another topic in speciation theory, namely, the degree to which reproductive isolating mechanisms arise in allopatric versus sympatric populations. In the warblers discussed here our findings indicate that much of the genetic differentiation of the speciation process, including that underlying the

evolution of potential isolating mechanisms, occurred in allopatry. This would not preclude refinement of the mechanisms if and when these close relatives eventually become sympatric. Such a model is in agreement with modern genetic evidence on the course of early species formation (Lewontin 1974).

In conclusion, despite identity of plumage carotenoid pigment and allopatric nesting distributions, strong differences in habitat preferences and in plumage pattern and color argue for the maintenance of the current specific status of these warblers until properly quantified data on vocalizations, displays, and general pairing behavior are available.

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