

# THE DETECTION OF NEAR-ULTRAVIOLET LIGHT BY NONMIGRATORY AND MIGRATORY BIRDS

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**ABSTRACT.**—Near-ultraviolet (UV) light reception was demonstrated for the first time in three species of nonmigratory emberizid and passerid birds. Behavioral data also established that eight additional alcedinid and emberizid birds can detect near-UV wavelengths. The finding that these more recently evolved species can see near-UV light implies that near-UV vision is probably an important visual capability in most, if not all, diurnal birds. Although the utility of near-UV reception for birds remains equivocal, the fact that nonmigratory as well as migratory birds can perceive UV suggests that birds may be able to utilize the UV spectrum for homing, orientation, and navigation, as do the UV-sensitive arthropods. It also can be inferred that UV vision may be especially useful to insectivorous birds for the detection of UV reflectance patterns, which many otherwise cryptic arthropods possess for mate recognition. Ultraviolet reflectance patterns also may be useful to frugivorous and nectarivorous birds for the detection of food items. *Received 17 January 1983, accepted 8 July 1983.*

NEAR-ULTRAVIOLET (UV) light reception was first demonstrated in the homing pigeon (*Columba livia*) by Kreithen and Eisner (1978), although an earlier study by Wright (1972) had indicated that UV light affected color discrimination in pigeons. Emmerton and Delius (1980) have confirmed that pigeons can discriminate UV wavelengths and have convincing data that imply that the pigeon's visual system may be tetrachromatic, or possibly pentachromatic. Goldsmith (1980) has shown that three species of hummingbirds (*Archilochus alexandri*, *Lampornis clemenciae*, and *Eugenes fulgens*) can see near-UV light, and we have found similar capabilities in the relatively primitive Mallard (*Anas platyrhynchos*) (Parrish et al. 1981). The fact that the lenses, ocular media, and some oil droplets of pigeons and other birds do not strongly absorb UV (Strother 1963, Govardovskii and Zueva 1977, Emmerton et al. 1980), as do the lenses and other optical components of UV-blind humans and many other animals (Walls and Judd 1933, Walls 1940, Wald 1952, Kennedy and Milkman 1956), prompted us to survey several groups of birds in order to determine whether or not, in general, most other birds also can see near-UV light.

The present studies were designed to determine whether or not near-UV light reception is found among nonmigratory groups of birds and to ascertain whether or not such visual capabilities are widely distributed among representatives of the more recently evolved fami-

lies of Alcedinidae, Emberizidae, and Passeridae (AOU Check-list 1982). Our behavioral data suggest that nonmigratory as well as migratory species of the most recently evolved passerines are capable of near-UV light detection.

## METHODS

All bird species were caught in live traps in the vicinity of Emporia in Lyon County, Kansas during the fall and spring of 1980 and 1981, with the exception of a female Belted Kingfisher (*Cerle alcyon*), which was delivered to the biology department after it had been slightly injured during a dive into a shallow stream. The birds were maintained indoors in wire cages after capture and were allowed free access to food and water during their temporary confinement.

Ultraviolet-light detection was determined in the Belted Kingfisher by use of a cardiac-conditioning technique according to previously described procedures (Parrish et al. 1981). The other birds were tested by employing either a key-pecking technique in a Skinner box or a shock-avoidance technique in a double-ended shuttle box in a dimly lighted room.

The key-pecking method involved placing the birds in a Skinner box (23 × 24 × 19 cm) constructed of wood painted flat black and plexiglass on the top and sides. The front of the box had a 4-cm-square opening, covered on the outside by a slightly larger piece of UV-transparent Pyrex glass that acted as the pecking key. Pecks on the illuminated glass key closed an electrical circuit and activated a solenoid. This in turn opened a tube that delivered a food reward into a tray inside the Skinner box. A manual control switch to the food solenoid was used during the initial key-peck training to white light (7 watt bulb). All birds

were deprived of food for 2–5 h before each experimental session. With 2–3-h daily training sessions, most birds were conditioned to the white light within 3–4 weeks. Once conditioned to the white light, the birds were given an additional day of training to monochromatic green light (560 nm), followed by monochromatic near-UV light between 350 and 365 nm. Activation of a silent, solid-state relay switched on the UV light, which was presented to the birds for 5–6 s at irregular 15–90-s intervals, according to signals recorded on a cassette tape. The light signals, key-pecking signals, and coincidence signals (generated when key-pecks occurred when the UV light was on) were recorded from an electronic control box on a Model Four Physiograph recorder. Monochromatic light was generated by passing ultraviolet light from either a GE Purple-X 250W or GE F15T8 BLB bulb through a Hitachi-Perkin Elmer Model 139 spectrophotometer. The monochromator had a built-in UV transmitting filter, which transmitted less than 0.1% light above 400 nm. An ultraviolet-absorbing, visible-transmitting filter (Corning CS 3-71; see Table 1) was occasionally inserted into the monochromator's exit-light pathway. This was done to insure that the positive responses of the birds were due to near-UV light reception and not to the small amount of spurious red-harmonic light passed by the low-band-pass, UV-transmitting filter. It should be noted that a dark-adapted human observer was unable to discern any red light under those conditions. In order to prevent reinforcement of noncoincident key-pecks, the food-solenoid was inactivated when the high-pass filter was inserted into the exit-light pathway.

The shock-avoidance method employed a double-ended shuttle box (81 × 30 × 46 cm) constructed of wooden ends, painted flat black, a plexiglass top and sides, a 20-cm-high middle-partition, which had a rotating (about 60 rpm) 2.5-cm-diameter dowel rod on top, and 4.8-mm-diameter brass rods spaced 6.4 cm apart in the floor. A 9.5-cm-diameter hole was cut in the center of each end, about 4 cm above the floor, with a bracket to hold a 10-cm-diameter Pyrex plate. A wide-band (about 320 to 380 nm), achromatic UV-light source of about 50  $\mu\text{W}/\text{cm}^2$  intensity was provided at one end by a GE F15T8 BLB lamp, which was filtered with a Schott UG-11 UV-transmitting filter, while monochromatic UV light (about 0.2  $\mu\text{W}/\text{cm}^2$  at 365 nm) was provided at the other end. This arrangement was necessitated because of the availability of only one monochromator. Light from either end was presented to the birds for 5–10 s, after which the appropriate floor grid was immediately energized, initially with about 0.5 milliamperes direct current (Gelman Instruments, power supply) and later with about 0.4 milliamperes alternating current (Lafayette Instruments, constant current shocker). Each bird was given an initial training period in the shuttle box for about an hour, after which it was

allowed a short rest period. Following the rest period, positive responses were recorded if the birds flew to the opposite end of the shuttle box, tried to perch on the rotating rod above the middle partition, or if they exhibited flight in the UV-lighted end of the shuttle box in order to avoid the impending mild shock. In order to insure that the birds were responding to the UV light stimuli and not to the potentially spurious red-harmonic light, the cut-off filter was occasionally inserted into the exit-light pathway of the monochromatic light source.

## RESULTS

*Nonmigratory birds.*—Blue Jays (*Cyanocitta cristata*), House Sparrows (*Passer domesticus*), and Northern Cardinals (*Cardinalis cardinalis*) all were found to detect near-ultraviolet light, regardless of whether they were tested in the shuttle box, where they exhibited greater than 90% positive responses (Table 1), or the Skinner box, where they showed 65% or greater coincidence (Table 2). The dramatic diminutions in the responses to less than 12% in all three species of birds in the presence of the UV-absorbing, visible-transmitting filter confirm that the birds were responding to UV light and not to the potentially spurious red-harmonic light transmitted by the high-pass filter (Tables 1 and 2).

*Migratory birds.*—Brown-headed Cowbirds (*Molothrus ater*) and Harris' Sparrows (*Zonotrichia querula*) both demonstrated 94% positive responses to near-UV light stimuli in the shuttle box (Table 1) and 70% or greater coincidence in the Skinner box (Table 2). Positive responses of greater than 91% also were obtained in the European Starling (*Sturnus vulgaris*), Common Grackle (*Quiscalus quiscula*), Dark-eyed Junco (*Junco hyemalis hyemalis*), American Tree Sparrow (*Spizella arborea*), and the White-crowned Sparrow (*Zonotrichia leucophrys*) tested with UV-light stimuli in the shuttle box (Table 1). Again, positive responses were greatly reduced in the presence of the high-pass filter (Tables 1 and 2). Ultraviolet light reception, in addition, was demonstrated in a female Belted Kingfisher by means of the cardiac-conditioning technique (Table 3). The insertion of the high cut-off filter into the exit-light pathway abolished the positive responses, substantiating that the positive responses were due to UV-light detection (Table 3).

TABLE 1. Shuttle-box responses of passerine birds to monochromatic UV light stimuli of 360 nm in the absence or presence of a UV-absorbing filter<sup>a</sup> or to achromatic near-UV light stimuli of 320-380 nm.<sup>b</sup>

Species (number) <sup>c</sup>	Positive responses/trials (percentage positive responses)			
	Mono- chromatic UV light	Achromatic UV light	Totals near-UV light	UV light with filter
Blue Jay (2)	62/66	75/82	137/148 (92%)	2/37 (5%)
House Sparrow (4 ♂, 1 ♀)	169/185	191/210	360/395 (91%)	3/86 (3%)
Northern Cardinal (1 ♂)	31/32	38/43	69/75 (92%)	1/14 (7%)
European Starling (2)	50/55	42/45	92/100 (92%)	2/39 (5%)
Common Grackle (2 ♂)	61/68	76/80	137/148 (93%)	2/37 (5%)
Brown-headed Cowbird (2 ♂, 1 ♀)	106/111	139/150	245/261 (94%)	3/61 (5%)
Dark-eyed Junco (2 ♂)	59/63	58/61	117/124 (94%)	0/45 (0%)
American Tree Sparrow (3)	69/73	84/88	152/161 (94%)	1/52 (2%)
Harris' Sparrow (4)	132/141	132/141	264/282 (94%)	3/70 (4%)
White-crowned Sparrow (1)	39/40	44/48	83/88 (94%)	0/12 (0%)

<sup>a</sup> The Corning filter (CS 3-71), which was occasionally inserted into the exit-light pathway, had 50% or better transmission of wavelengths above 480 nm but less than 0.1% transmission below 460 nm.

<sup>b</sup> Achromatic UV light was provided by a GE F18T8-BLB filtered by a Schott UG-11 filter, which had 55% or greater transmission between 320 and 380 nm but less than 1% transmission above 400 nm.

<sup>c</sup> Sex is indicated in dimorphic species: ♂ = male, ♀ = female.

## DISCUSSION

Our results, indicating that Northern Cardinals, House Sparrows, and Blue Jays can detect near-ultraviolet light (Tables 1 and 2), represent the first demonstrations of UV-detection capabilities among nonmigratory or nonhom-ing populations of avian species. It should be noted, however, that, although adult Blue Jays are nonmigratory in Kansas (Johnston 1964), they commonly are migratory in their northernmost ranges (Lincoln and Peterson 1979). Young Blue Jays, likewise, are known to disperse in small flocks during the fall and spring in the Great Plains (Johnston 1964, Johnsgard 1979). Similarly, the otherwise nonmigratory House Sparrow apparently exhibits migratory habits in China (Welty 1982). In marked contrast, the Northern Cardinal is relatively sedentary and, in Kansas, only occasionally ranges beyond about 1 km from its home territory (Fitch 1958). Although there are reports of possible migration of Northern Cardinals in Ohio (Campbell 1968) and Illinois (Graber and Graber 1963), a recent study by Kloek (pers. comm.) indicates that cardinals do not appear to be migratory in Illinois.

Our results additionally present evidence that starlings, grackles, cowbirds, juncos, sparrows, and the kingfisher can be added to the list of migratory species of birds that can detect near-UV light (Tables 1, 2, and 3). The demonstra-

tions of near-UV light reception in the primitive Anseriformes (Parrish et al. 1981), the more recently evolved Columbiformes (Kreithen and Eisner 1978), Apodiformes (Goldsmith 1980), and Coraciiformes (Table 3), and the most recently evolved Passeriformes (Tables 1 and 2) imply that near-UV light is probably an important visual component of the light spectrum in most, if not all, diurnal birds. Whether or not birds with nocturnal habits (rod-dominated retinas) possess similar capabilities needs to be determined. We have begun these investigations in our laboratory.

The appreciably lower percentage of positive responses (key-pecks) of the birds in the Skinner-box experiments than in the shuttle-box experiments should not be construed to mean that the birds were less sensitive to UV light under the former conditions. There are several factors that are probably responsible for these differences. First, the experiments involved two entirely different behavioral paradigms, and the birds would not be expected to perform equally well under both types of experimental conditions. Second, the birds in the Skinner box were not given a shock following incorrect responses, as they were in the shuttle box. Third, it is well established that task-oriented learning constraints exist in pigeons (see Delius and Emmerton 1979), and similar constraints are probably present in other birds too. Fourth, it is probable that the percentage coincident key-

TABLE 2. Key-peck responses of male passerine birds to monochromatic UV light stimuli in the absence or presence of a UV-absorbing filter.<sup>a</sup>

Species (number)	Wavelength	Coincident pecks/light stimuli (% coincidence)	
		UV light	UV light with filter
House Sparrow (1)	350 nm	259/506 (65%)	30/234 (11%)
Northern Cardinal (2)	350 nm	281/618 (70%)	2/222 (11%)
Brown-headed Cowbird (2)	350/360 nm	575/613 (70%)	6/75 (13%)
Harris' Sparrow (1)	365 nm	42/71 (79%)	12/224 (16%)

<sup>a</sup> The Corning filter (CS 3-71), which was occasionally inserted into the exit-light pathway, had 60% or better transmission of wavelengths above 480 nm but less than 0.1% transmission below 460 nm.

pecks could have been increased in the operant conditioning experiments, but we did not require that the birds achieve 90–100% positive responses before beginning data collection. Finally, the birds were tested in the Skinner-box experiments before we began the shuttle-box experiments and had been released to the wild before we realized that there were going to be fairly large differences in the percentage responses between the two experimental paradigms. Because the birds tested in the Skinner-box tested birds had already been released, they were not available for retesting.

The utility of UV vision to birds is not known, but near-UV light is *sine qua non* for the detection of the sun behind obscuring clouds, for orientation to polarized UV-light patterns in a clear sky, and for the detection of UV-reflectance patterns on flowers and invertebrate mates (von Frisch 1967, Wehner 1976). Homing pigeons previously have been shown to detect polarized-visible light (Kreithen and Keeton 1974; Delius et al. 1976) and, more recently, polarized-UV light as well (Kreithen, pers. comm.). The ability of pigeons to detect polarized-UV light does not necessarily imply that UV is used similarly in birds and invertebrates, but the likelihood seems great, as both birds and insects are highly mobile, and both groups possess excellent homing and migratory capabilities. While bees home quite well under partially overcast skies (von Frisch 1967), the situation is not as clear in birds. Clock-shifted pigeons, for example, exhibit predictable, deflected, vanishing bearings when released under sunny skies but show nonrandom, homeward, vanishing bearings when released under totally overcast skies (Keeton 1969). These results have been important in suggesting that pigeons also may possess nonvisual orientation mechanisms. It would be of particular interest

to examine the vanishing bearings of clock-shifted pigeons released on partially cloudy days, with clear patches of blue sky, in order to confirm their use of polarized-UV light from the blue sky in orientation. Because experimental design limitations appear to account for the fact that House Sparrows and other non-migratory birds exhibit poor homing abilities (Matthews 1968), it is, indeed, likely that all diurnal birds can use UV wavelengths to orient themselves spatially within a range that may be limited to a few kilometers or extended to hundreds or even thousands of kilometers, as in homing and migratory species. In addition to the utility of near-UV light for orientation among nonmigratory and migratory birds, its use for the detection of UV-reflectance patterns on arthropod prey species also may be important, particularly in the many birds, such as the Northern Cardinal and the Blue Jay, that shift from primarily granivorous to increased insectivorous habits in the spring (Martin et al. 1951). Near-UV vision also may be important in frugivorous birds, as Burkhardt (1982) has recently shown that many berries strongly reflect UV light. While the presence of strong UV-reflec-

TABLE 3. Cardiac responses of greater than 19 beats/min in a Belted Kingfisher conditioned to monochromatic UV light of 360 nm in the absence or presence of a UV-absorbing filter.<sup>a</sup>

Sex	Positive responses/trials (% positive responses)	
	UV light	UV light with filter
Female	17/19 (89%)	0/5 (0%)

<sup>a</sup> The Corning filter (CS 3-71), which was occasionally inserted into the exit-light pathway, had 60% or better transmission of wavelengths above 480 nm but less than 0.1% transmission below 460 nm.

tance patterns has recently been demonstrated to be especially strong in white feathers (Burkhardt 1982, Parrish unpubl.), it is doubtful that birds make use of these patterns for mate recognition, because the males of most species readily advertize their sex by visible-reflectance patterns or colors, songs, courtships, or other behavioral mechanisms. One of us has surveyed museum specimens of visibly nondimorphic species for sexual differences in near-UV reflectance patterns with a videocamera and was unable to discern any marked differences between the sexes (Parrish unpubl.). Whether or not such patterns also are absent in living, sexually nondimorphic specimens needs to be examined.

The ability of birds to detect near-UV wavelengths is not surprising, as it is well documented that the optical media of birds are capable of transmitting near-UV spectra (Emmerton et al. 1980). That a similar capability is not present in man is due to the yellow, intraocular lens filters, because aphakic (lensless) humans can read an eyechart with UV light (Wald 1952). The latter results imply that a special photopigment is not necessarily needed for UV vision. Available evidence indicates, however, that pigeons and chickens possess a short-wavelength-sensitive visual pigment with an absorption maximum near about 415 nm (Govardovskii and Zueva 1977, Fager and Fager 1981). While these results suggest that UV vision in diurnal birds may be a result of a specific UV-receptor, there are currently no data available to confirm this possibility.

The cumulative data to date thus imply that UV vision may be a standard component of the visual system of diurnal birds, although there is only conjecture about its possible adaptive significance. Initially, it might be fruitful to investigate uses of UV vision in birds similar to those already demonstrated in insects. There may be other uses that are specific to birds, however, due to the many complex components of the avian visual system. While the opulence of the world of UV vision is masked by our own inability to see it, it is visibly clear that further research is necessary to allow us to discern the importance of UV-vision to the ecology and physiology of the birds.

#### ACKNOWLEDGMENTS

We thank David Bainum for the design and construction of the electronic control box used in the

Skinner-box experiments. We also would like to express our gratitude to the referees for their many invaluable suggestions. This research was supported in part by a grant from the Emporia State University Research Committee to J. Parrish.

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1982. Check-list of North American Birds, 34th Supplement. *Auk* 99: 1-16cc.
- BURKHARDT, D. 1982. Birds, berries and UV: A note on some consequences of UV vision in birds. *Naturwissenschaften* 69: 153-157.
- CAMPBELL, L. 1968. *Birds of the Toledo area*. Toledo, Ohio, Toledo Blade Press.
- DELIUS, J. D., AND J. EMMERTON. 1979. Visual performance of pigeons. Pp. 51-70 in *Neural mechanisms of behavior in the pigeon*. (A. M. Granda & J. H. Maxwell, Eds.). New York, Plenum Publ. Corp.
- , R. J. PERCHARD, & J. EMMERTON. 1976. Polarized light discrimination by pigeons and an electroretinographic correlate. *J. Comp. Physiol. Psychol.* 90: 560-571.
- EMMERTON, J., & J. D. DELIUS. 1980. Wavelength discrimination in the "visible" and ultraviolet spectrum by pigeons. *J. Comp. Physiol.* 141: 47-52.
- , J. SCHWEMER, I. MUTH, & P. SCHLECHT. 1980. Spectral transmission of the ocular media of the pigeon (*Columba livia*). *Invest. Ophthalmol. Vis. Sci.* 19: 1382-1387.
- FAGER, L. V., & R. S. FAGER. 1981. Chicken blue and chicken violet, short wavelength sensitive visual pigments. *Vision Res.* 21: 581-586.
- FITCH, H. S. 1958. Home range, territories, and seasonal movements of vertebrates of the Natural History Reservation. *Univ. Kansas Publ. Mus. Nat. Hist.* 11: 63-326.
- GOLDSMITH, T. H. 1980. Hummingbirds see near ultraviolet light. *Science* 207: 786-788.
- GOVARDOVSKII, V. I., & L. V. ZUEVA. 1977. Visual pigments of chicken and pigeon. *Vision Res.* 17: 537-543.
- GRABER, R. R., & J. W. GRABER. 1963. A comparative study of bird populations in Illinois, 1906-1909 and 1956-1958. *Illinois Hist. Surv. Bull.* 28: 383-528.
- JOHNSGARD, P. A. 1979. *Birds of the great plains*. Lincoln, Nebraska, Univ. Nebraska Press.
- JOHNSTON, R. F. 1964. *The breeding birds of Kansas*. Univ. Kansas Publ. Mus. Nat. Hist. 12: 575-655.
- KEETON, W. T. 1969. Orientation by pigeons: is the sun necessary? *Science* 165: 922-928.
- KENNEDY, D., & R. D. MILKMAN. 1956. Selective light absorption by the lenses of vertebrates, and its influence on spectral sensitivity. *Biol. Bull.* 111: 375-386.
- KREITHEN, M. L., & T. EISNER. 1978. Ultraviolet light

- detection by the homing pigeon. *Nature* 272: 347-348.
- , & W. T. KEETON. 1974. Detection of polarized light by the homing pigeon, *Columba livia*. *J. Comp. Physiol.* 89: 83-92.
- LINCOLN, F. C., & S. R. PETERSON. 1979. Migration of birds. U.S. Dept. Interior/Fish Wildl. Serv., Circ. 16.
- MARTIN, A. C., H. S. ZIM, & A. L. NELSON. 1951. American wildlife and plants. New York, Dover Publ.
- MATTHEWS, G. V. T. 1968. Bird navigation, 2nd Ed. Cambridge, England, Cambridge Univ. Press.
- PARRISH, J., R. BENJAMIN, & R. SMITH. 1981. Near-ultraviolet light reception in the Mallard. *Auk* 98: 627-628.
- STROTHER, G. K. 1963. Absorption spectra of retinal oil globules in turkey, turtle and pigeon. *Exp. Cell Res.* 29: 349-355.
- VON FRISCH, K. 1967. The dance language and orientation of bees. Cambridge, Massachusetts, Harvard Univ. Press.
- WALD, G. 1952. Alleged effects of the near ultraviolet on human vision. *J. Opt. Soc. Amer.* 42: 171-177.
- WALLS, G. L. 1940. The pigment of the vertebrate lens. *Science* 91: 172.
- , & H. D. JUDD. 1933. The intra-ocular colour filters of vertebrates. *British J. Ophthalmol.* 17: 641-675, 705-725.
- WEHNER, R. 1976. Polarized-light navigation by insects. *Sci. Amer.* 235: 106-115.
- WELTY, J. C. 1982. The life of birds, 3rd Ed. Philadelphia, Saunders Publishing Co.
- WRIGHT, A. A. 1972. The influence of ultraviolet radiation on the pigeon's colour discrimination. *J. Exp. Anal. Behav.* 17: 325-337.