grasshoppers such as *Phlaeoba*, whose locomotion has a large vertical component, have their bands oriented horizontally, while larger migratory and flying species have their bands oriented vertically. (The latter typically have finer bands than the former.)

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Hummingbirds See Near Ultraviolet Light

Abstract. *Three species of hummingbird (*Archilochus alexandri, Lampornis clemenciae, *and* Eugenes fulgens*) were trained to make visual discriminations between lights of different spectral content. On the basis of initial choices of feeders following a period of conditioning, birds of all three species were able to distinguish near ultraviolet (370 nanometers, 20-nanometer half bandwidth) from darkness (unilluminated viewing screen) or from the small amount of far red light that leaked through the ultraviolet-transmitting glass filter. A human observer was unable to make either discrimination. The birds were also able to distinguish white lights lacking wavelengths shorter than 400 nanometers from the full spectrum of the quartz-halogen bulbs. One can infer that the cone oil droplets, which have been lost from the retinas of most mammals, provide a potentially more flexible system for restricting the short wavelength end of the visible spectrum than does the filtering action of lens and macula that serves this function in the human eye.*

The visible spectrum for the human eye does not extend into the near ultraviolet (UV). The physical reason is that the lens absorbs wavelengths shorter than about 400 nm and the central area of the retina contains a yellow patch of carotenoid-containing cells, the macula lutea, which also filters out the violet rays (*1*). These features are generally believed to be evolutionary answers to the inevitable problem of chromatic aberration in the refractile elements of the eye. Because chromatic aberration becomes increasingly severe as wavelength decreases, visual acuity is significantly enhanced by the presence of these short wavelength absorbing filters (*2*). The modest price is a sacrifice in sensitivity to the shortest wavelengths available in the terrestrial solar spectrum. For insects, in contrast, whose eyes are assembled on a different optical principle, chromatic aberration is not a problem, and receptors specifically sensitive to near UV are frequently present (*3*).

Among the lower vertebrates, restrictions on sensitivity to short wavelengths appear common, at least in diurnal forms. Yellow lenses are common (*4*), and the densely colored cone oil droplets that are such prominent features of the retinas of birds and reptiles have often been interpreted as long-pass filters that reduce the effects of chromatic aberration (*5, 6*). Until recently there has been little evidence that the eyes of vertebrates are normally sensitive to near UV light, but reports exist for toads (*7*), newts (*8*), and lizards (*9*). The ocular media of chickens and pigeons are transparent to much of the near UV (*10*), and pigeons (*Columba livia*) see in this spectral region (*11, 12*). The action spectrum reported by Kreithen and Eisner (*12*) is noteworthy because the threshold in the UV is lower than the peak in the visible range and cannot therefore be attributed to fluorescence or absorption by a rhodopsin *cis* peak.

I now report behavioral experiments demonstrating sensitivity of hummingbirds to near UV light (*13*). The experiments exploit the fact that hummingbirds can be attracted readily to artificial feeders and can be taught by differential reinforcement to make discriminations between feeders. The experiments were done in the Chiricahua Mountains in southeastern Arizona, on three species of hummingbird: the black-chinned (*Archilochus alexandri*), the blue throated (*Lampornis clemenciae*), and magnificent or Rivoli's (*Eugenes fulgens*). By netting and marking individual birds, the population size of *A. alexandri* was estimated to be about 90, and the frequencies of visitation of individual birds was measured (*14*). The visiting population can be retrained to a new discrimination in less than 1 day, and in making discriminations, hue is demonstrably more important than brightness (*14*).

Four feeders were mounted on photographic tripods at a height of about 1 m and in a row about 0.6 m apart. Each consisted of a matte black metal box (20 by 18 by 25 cm) containing a 500-watt quartz-halogen projector lamp run from a stabilized power supply, heat and neutral density filters, collimating lenses, and filters to alter the spectral composition of the light. At each feeder, the light irradiated a 22-mm ground glass disk on the front of the box, located about 1.5 cm behind the stem of a plastic feeding bottle. The birds viewed this luminous disk both while approaching the feeder and while hovering to drink. Sugar solution (30 percent sucrose) was supplied at two of the feeders (training light) and $0.5M$ NaCl at the others (test light) (*15*). Test and training lights appeared at alternate positions in the array of four feeders, and the positions were interchanged at regular intervals to prevent the birds from locating the correct feeder by position rather than spectral content of the light.

Near UV light was generated with a Corning CS 7-37 filter, which transmits a broad band of wavelengths (λ) with a maximum at 360 nm. Because of the emission characteristics of the lamps, the maximum in the spectral distribution

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of the stimulus was shifted to about 370 nm. The full band was 350 to 390 nm. The flux of near UV light in a plane just external to the viewing port was about 6×10^{13} photon $\sec^{-1}$ cm^{-2} (*16*).

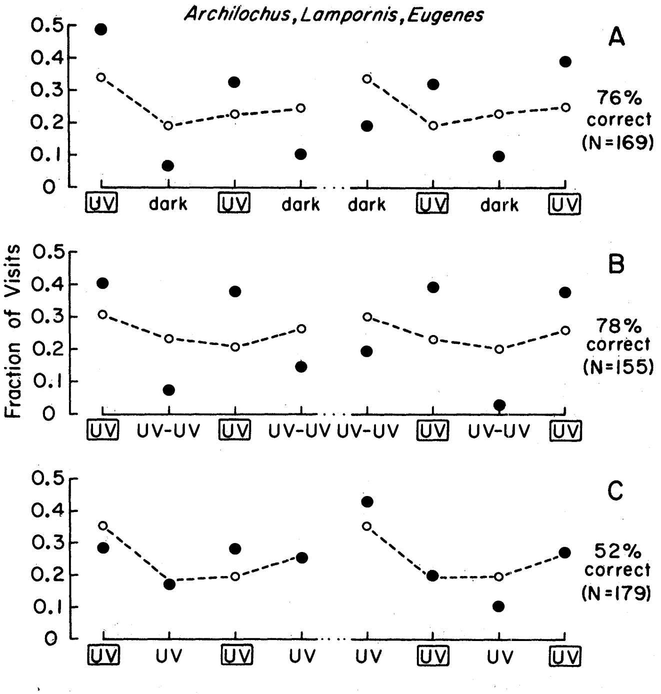
A human observer viewing the apparatus from the front was unable to distinguish this UV light from adjacent feeders in which the lamps were not burning ("dark"). After training to the UV stimulus the birds were able to detect a difference and tracked the UV light with 76 percent accuracy (Fig. 1).

The UV-transmitting glass filter used in these experiments has a low leak in the far red, which, although not visible to a human observer during daylight hours, was detectable after sunset. A second experiment was therefore done to test whether the birds were selecting the feeders on the basis of the UV rather than the weak far red or infrared component of the stimulus (Fig. 1B). For this experiment all lamps were fitted with UV glass filters and were lit, but, in addition, the test lights also had long-pass glass filters that absorbed all wavelengths shorter than 405 nm (Corning CS 3-74). These filters were placed behind the UV filters, so that any fluorescence was absorbed by the latter. Training (UV) lights and test (UV minus UV) lights were therefore virtually identical in the trace of far red light they contained, but only the training light included near UV wavelengths. The birds made the discrimination with slightly better fidelity (78 percent correct) (Fig. 1B) than in the first experiment.

A third experiment was undertaken to ensure that the discriminations were based on the spectral characteristics of the light sources rather than on some other difference in the feeders or on memory of position. When the UV stimulus was presented at all viewing ports, the birds selected the sugar bottles with only 52 percent accuracy, or no better than chance (Fig. 1C) (*17*). The experiments of Fig. 1 therefore demonstrate that the visible spectrum of hummingbirds extends into the near UV, to shorter wavelengths than the visible spectrum of human beings.

The data in Fig. 1 are pooled results for all three species. The 60 percent of the visits by black-chinned hummingbirds were analyzed separately, with virtually the same result: choices were 76 percent correct in both Fig. 1, A and B. The vision of all three species of hummingbird that were using the feeders therefore extends into the near UV.

A fourth experiment was performed to see whether the birds could distinguish white light lacking the UV component from the full spectrum of the quartz-halogen lamps. The long-pass Corning CS 3-74 filters were used to remove the UV from the test lights. Unlike the test and training lights used in the experiments of Fig. 1, in this instance a human observer could see a small difference. The lights with the pale yellow long-pass filters appeared slightly warmer in hue. Not surprisingly the birds, too, could detect a difference (Fig. 2), but their accuracy in tracking the sugar was somewhat



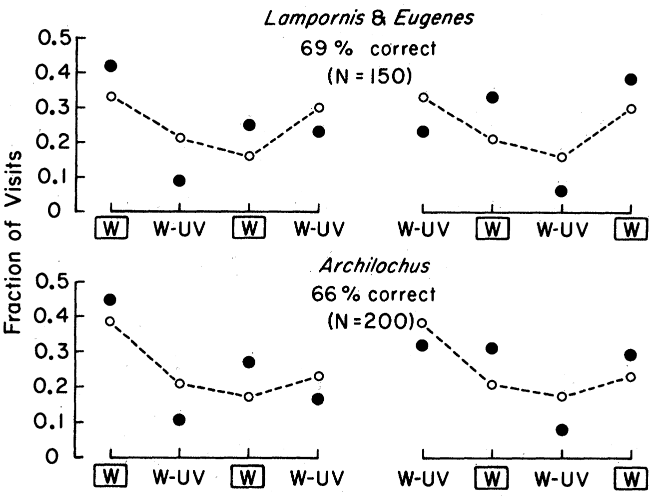


Fig. 1 (left). Distribution of initial visits among the feeders after training to UV light. In each of three separate experiments (A, B, and C) the birds received sucrose only at those feeders where the designation of the stimulating light is enclosed in a rectangle below the abscissa. *UV*, 350 to 390 nm (CS 7-37 filter); *dark*, same but lamp not burning; *UV-UV* (UV minus UV), was 350 to 390 nm (CS 7-37) blocked with a pale yellow long-pass filter (CS 3-74). In each experiment, the positions of the feeders were switched before counting started and after each block of 25 visits by black-chinned hummingbirds (*Archilochus alexandri*). Counting stopped after 100 tabulated visits. By shifting the feeders in this manner, the birds were unable to use position to identify the location of the sugar [(*14*) and (C)]. Right and left halves of (A), (B), and (C) show the distribution of visits for each of the two arrangements of test and training lights. Small open circles and broken lines show the distribution of all visits (pooled data for the two arrangements of lights). The birds tend to favor the end feeders, particularly the left end. Deviation of the large filled circles from these distributions indicates the birds' ability to find the sugar bottles on the basis of perceived differences in the lights. (A) Training light UV; test light dark. For each half of the graph, the frequencies of visits to the UV viewing ports lie above the broken curve; visits to the unilluminated feeders lie below the curve. The initial visits were 76 percent correct in locating the sugar. Deviations of observed (large filled circles) from expected (broken curve, position effect) are highly significant by a chi-square test ($P < .01$). (B) A similar experiment to (A) in which the test light was UV minus UV. That is, the UV filter was supplemented with a pale yellow filter (CS 3-74) that passes only the far red leak from the UV filter. As in (A), the birds tracked the UV light. Accuracy was 78 percent, and departure from chance is highly significant (chi-square test; $P < .01$). (C) When feeders were identical except for the presence of sugar, the birds located the sucrose solutions on initial visits no more frequently than chance (52 percent correct; deviations from the average position effect occur in both directions and are not statistically significant). The discriminations exhibited in (A) and (B) were therefore based on the differences in spectral quality of the lights and not some other feature of the feeders. Fig. 2. (right). An experiment similar to those of Fig. 1, except that the training light was white light (slightly tinted by heat filters) and the test light was the same, supplemented by filters absorbing below 405 nm (CS 3-74). Feeder positions were shifted after every 25 counts of *Archilochus* to prevent the birds from learning position. Lights had a brightness roughly equal to monochromatic yellow, with a quantum flux of 10^{15} photon $\sec^{-1}$ cm^{-2}.

less impressive than when they employed the probably more saturated (but to us invisible) wavelength band in the near UV (Fig. 1, A and B).

Cone oil droplets contain such high concentrations of carotenoids that the redder droplets have absorbances of 50 to 90 and the paler droplets more than 3 (*18*). Even the latter, however, implies a significant absorption in the near UV. How, then, does UV light reach the photoreceptors? One possibility is that rods, which lack oil droplets, are mediating the response. Although in pigeons the accessory members of double cones also lack an oil droplet, their outer segments contain a visual pigment with $\lambda_{\max}$ at long wavelengths, near 570 nm (*6*). Nevertheless, UV sensitivity may involve receptors more specifically sensitive to short wavelengths than either rods or long wavelength cones. In turtles, there are two subclasses of colorless droplet, one of which is transparent in the near UV (*19*). Moreover, recent evidence from pigeons indicates the presence of a cone with $\lambda_{\max}$ at 400 or 415 nm (*10, 20*). These findings suggest that UV vision by hummingbirds could be mediated by a photopic mechanism, and a receptor with $\lambda_{\max}$ in the near UV is not precluded (*12*).

The sensitivity of birds to UV light invites speculation about its adaptive significance, a tack that implies that the human retina represents the standard of performance against which diurnal visual systems should be measured. By this reasoning if an animal can see in the UV, there must have been some special evolutionary pressures that created the capacity, and the roots can be discovered by digging into the behavioral ecology of the species. There is also an alternative view, whose origins are to be found in the writings of Walls (*2*). The early mammals were most likely nocturnal creatures, and color vision in the mammalian line has become largely degenerate. The Old World primates, ourselves included, are the most notable exceptions, but in our evolutionary line cones and color vision have secondarily resurged, hand in hand with the adoption of diurnal habits. Moreover, all of the contemporary groups of placental mammals have lost the retinal oil droplets, and oil droplets once lost have never been recovered in evolution (*2*). Oil droplets provide a very selective form of filter, enabling individual cones to be screened. In principle, therefore, they may be arranged so as to permit the retinas of birds and reptiles to maintain the utmost in visual acuity without sacrificing all cells that are sensitive to the shortest wavelengths in the environment. Although we clearly must know more about the retinal distribution of avian UV receptors—for example, whether they are present in the foveas—one is reminded that in an evolutionary sense our color vision system has most likely been reconstructed from a photopically less capable retina, from which some of the original parts were lost forever. In this view, our retina is therefore making the best of a suboptimal situation, and it is the avian retina that comes closer to being the diurnal retina par excellence. This realization should leave us more open to the discovery of unsuspected visual capacities in other animals. More specifically, the interplay of several spectral classes of oil droplets with several cone pigments and the presence of receptors functioning in the near UV suggest that avian color vision possesses a richness that lies beyond our ken.

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Nursing Frequency, Gonadal Function, and Birth Spacing Among !Kung Hunter-Gatherers

Abstract. *Mothers among !Kung hunter-gatherers nurse briefly and frequently, with brief intervals between nursing bouts (mean ± standard error, 13.19 ± 1.28 minutes). The low levels of 17β-estradiol and progesterone in the serum of the mother are correlated with infant's age and with interbout interval, but not with total nursing time. Maternal gonadal function is apparently suppressed by a timing-dependent, prolactin-mediated effect of breast stimulation. Interbout interval may be a key variable in lactation infertility. If so, it solves the puzzle of !Kung birth spacing.*

Nursing markedly lengthens birth spacing in a number of noncontracepting, nonindustrial populations. Mean postpartum amenorrhea is less than 2 months in women who do not nurse, but at least 10 and up to 18 months in nursing women. In addition, the interval from the onset of menses to conception is lengthened by nursing (*1*). In some noncontracepting, nonabstinent populations where very late weaning is the custom, birth spacing is longer than 3 years.

One probable mechanism by which nursing influences fertility is a direct or indirect effect of prolactin on gonadal function (*2-9*). Prolactin is promptly secreted in response to nipple stimulation in human females, increasing 2- to 20-fold in plasma during 5 to 15 minutes of mechanical stimulation of the nipple (lac-