**Laird, Molly**

THE ROLE OF RETINAL OIL DROPLETS IN COLOR VISION IN THE PIGEON

*City University of New York* PH.D. 1986

**PLEASE NOTE:**

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark ✓.

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print ✓
3. Photographs with dark background ✓
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages ✓
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Dissertation contains pages with print at a slant, filmed as received _____
16. Other _____

_____

_____

University
Microfilms
International

# THE ROLE OF RETINAL OIL DROPLETS IN COLOR VISION IN THE PIGEON

by

Molly Laird

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements of the degree of Doctor of Philosophy, The City University of New York

1986

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

8/7/86
date

James Gordon
Chairman of Examining Committee

August 12, 1986
date

Herbert S. Sal[illegible]
Executive Officer

James Gordon

Peter Moller

Robert L. Thompson

The City University of New York

# Abstract

The Role of Retinal Oil Droplets in Color Vision in the Pigeon

by

Molly Laird

Adviser: Dr. James Gordon

The retinas of diurnal birds are characterized by the presence of intensely and vividly pigmented oil droplets located in the inner segments of cones. These droplets are pigmented by carotenoids. In order to clarify the possible role of these oil droplets in color vision, pigeons were reared on a carotenoid-free diet in an attempt to produce birds with colorless oil droplets. Because so much information is available about color vision in normal pigeons, this species seemed a promising subject for investigating the function of oil droplets.

Four normal birds and one bird reared on the diet were compared on a two-alternative forced choice wavelength discrimination task at 600 nm, the pigeon's area of best wavelength discrimination. The normal birds were also tested at 500 and 560 nm. Performance for the normal birds was essentially error-free down to intervals of about 4 nm at wavelengths both longer and shorter than the standard. The carotenoid-deprived bird did not learn the discrimination at

wavelengths longer than 600 nm for intervals as large as 20 nm. He did learn to discriminate a wavelength interval of 30 nm between 600 nm and shorter wavelengths, but performance rapidly fell to chance levels at wavelength intervals smaller than 25 nm.

A control for effects of intensity indicated that the birds ignored intensity information until virtually no wavelength information was available. Attempts to train birds on an intensity-only task while holding wavelength constant were only partially successful.

Electroretinographic testing of the retinal red field of the carotenoid-deprived and normal birds indicated that spectral sensitivity fell off much more steeply at wavelengths longer than 620 nm for the carotenoid-deprived than for the normal birds. Maximum sensitivity was shifted to 600 nm compared to 620 nm for the normal birds, and sensitivity was higher at 560 and 540 nm for the carotenoid-deprived bird than for the normal birds.

The amplitude of the ERG responses as well as their waveforms were normal for the carotenoid-deprived bird and provide evidence that retinal elements other than the oil droplets were unaffected by the dietary treatment. Microscopic examination of the experimental bird's retina showed that yellow and orange pigmented oil droplets were present but that the red droplets were absent.

This study indicates that one function of the red oil droplets is to sharpen wavelength discrimination at the

spectral area around 600 nm.

The Sheik

January 25, 1983 - May 28, 1986

## Acknowledgments

First I must express my gratitude to my subjects. They command my profoundest admiration not only for their extraordinary sensory capabilities, but also for their unfailing diligence and good temper.

I am grateful to my advisor, Dr. James Gordon, for his help in many areas. His knowledge of optics, the physics of light, and instrumentation is encyclopedic, and I could never have conducted the experiment without his assistance.

Dr. Robert Thompson was helpful on many occasions during the course of this study, particularly in suggesting ways for more effectively training the birds. His kindness, humor, and wisdom were steadying.

I am indebted to Dr. Peter Moller for his enthusiasm and energy. If it had not been for his encouragement I would have faltered on several occasions.

Dr. Katherine Fite, in addition to serving as outside reader, conducted histological investigations which were very useful to the study, and I am grateful to her.

Dr. Patricia Blough lent me the recording electrode for the ERG study, and offered me very useful advice and encouragement.

Dr. Martin Chodorow was helpful in suggesting ways of analyzing my results, and I am grateful for his

patience and knowledge.

The staff of the Academic Computing Department, particularly Andrew Blaner and Henry Wong, deserve my thanks for their patience, knowledge, and courtesy.

I am grateful to my friend Meredith Platt for her invariably wise counsel and support. My friend Patricia Zaleski also deserves my gratitude for her support. She was always helpful, good humored, and encouraging.

I thank the Animal Care staff, especially Ray Ferranti, for their conscientious work. Dan Cronin, Lab Technician, was always willing and capable, and I am grateful to him.

Frances Dolled and Irene Woerner were helpful to me on many occasions, and I thank them for their friendliness.

Finally, I would like to thank my husband, Harvey Slutsky, and daughter, Rachel Laird, for their support and encouragement during the years I conducted the study. They made many sacrifices for me and my work, and I will always be grateful to them.

# Table of Contents

## List of Tables

## List of Figures

# Introduction

It is known that diurnal birds have well-developed color vision capabilities, and for at least one species, the pigeon (Columba livia), there is considerable information about spectral regions of best discrimination, hue-shift functions, hue categorization, and saturation discrimination. Physiological mechanisms underlying color vision are coming to be understood; in recent years a number of cone pigments have been measured in birds. The existence of vividly and variedly colored droplets in the inner segments of cones of diurnal birds has been known for something over a century (e.g., Hannover, 1840). Yet the role of the droplets in the vision of birds (or, for that matter, of other animals), remains unexplained. The intense coloration of the droplets, their high optical density, and their location in the cones and thus in the pathway of the light stimulus, all argue that they play a role in color vision.

## Oil Droplets

The chemical composition of the droplets is imperfectly understood. Most of the carotenoids found in the oil droplets are xanthophylls (Goldsmith, Collins & Light, 1984), found in the retina as esters. The red droplet is the only one that has been identified with a carotenoid (astaxanthin) of known structure. In addition to the colored droplets, there are colorless droplets; these seem to contain no carotenoid.

It had been thought that the oil droplets were found only in diurnal species of birds; recently, however, droplets have been found in nocturnal species also, such as the tawny owl (Bowmaker, 1979). Nocturnal species typically have more colorless than pigmented droplets (Lythgoe, 1971). Oil droplets are also found in other vertebrates - in fish such as chondrosteans and dipnoeans, in amphibians and reptiles, and in monotremes and marsupials (Muntz, 1972). All these groups have colorless droplets; yellow and orange droplets are found in amphibians, reptiles, and birds. Only birds and turtles have red droplets (Muntz, 1972).

Ontogenetic studies of the oil droplets are available for three species of lizard (Dücker & Tiemann, 1972), for Japanese quail (Konishi, 1965), and for chick (Cooper & Meyer, 1968). Dücker and Tiemann

noted that the retinas of young (< three month) blindworms (Anguis fragilis) are characterized by colorless droplets, whereas droplets in the same area of adult retinas are yellow. The oil droplets of young sand lizards (Lacerta agilis) appear to be indistinguishable from those of adults in terms of color, though the droplets increase in size with age. The adult common lizard (L. vivipara) has orange, yellow, and colorless oil droplets; newly born lizards of this species show only colorless, yellow, and pale yellow droplets. Between the 21st and 25th day "chrome yellow" droplets appear, and by eight weeks the oil droplets appear identical to those of adults. Since the number of colorless droplets diminishes during development, Dücker and Tiemann propose that some of the colorless droplets become yellow; similarly, the number of yellow droplets present at birth also decreases, suggesting that orange droplets develop from the yellow ones.

Konishi (1965) classified droplets in the developing Japanese quail on the basis of the wavelength at which they are most sensitive ($\lambda$ max) into six types:(1) colorless; (2) green; (3) no peak between 400 and 500 nm; (4) three peaks between 400 and 500 nm; (5) red; and (6) orange. Types 1 and 3 first appeared on the 12th day after incubation followed by type 5; just before hatching types 2 and 6 appeared. Type 4 was

found on the 15th day. Types 5 and 6 do not derive from types 1 and 3, but arise independently. Green seems to arise from types 1 or 3 and orange from type 4.

Cooper and Meyer (1968) studied ontogeny of the chick's oil droplets. They arise in the following sequence: golden yellow, yellowish green, and red. They are detected spectrophotometrically before they can be seen by means of light microscopy. The yellow droplets appear first, at morphological stage 27 (5 days' incubation time); the yellow-green ("galloxanthin") are present at stage 34 (8 days). Concentrations of golden yellow and yellowish-green carotenoids begin to increase rapidly at stage 37 (11 days), when the inner segments are differentiating, but the oil droplet vacuoles have not yet appeared. The red pigment (astaxanthin) is present at stage 41 (15 days), at which time the retina possesses adult stratification: all ten layers are present and oil droplet vacuoles are observed for the first time. Comparable data for the pigeon are not available.

## Mechanisms of Color Vision in the Pigeon

Cone pigments. The existence of multiple cone pigments in birds was difficult to demonstrate, because the smallness and fragility of the cones made it

difficult to extract their pigments or to measure them by the technique of shining a beam of light through a single cone and measuring the amount of pigment absorbed (microspectrophotometry) (Govardovskii & Zueva, 1977). It is now known that the pigeon has at least four and possibly five cone pigments, and five types of oil droplets, arranged in specific and invariate combination with the cones. The distribution of the droplet-cone pairs across the retina is uneven, with a higher concentration of red and especially orange droplets located in the dorsotemporal quadrant, or red field, of the retina (Bowmaker, 1977). This red field is used in frontal, binocular, vision, as when the bird is feeding (Goodale, 1983). The yellow field comprises the remainder of the retina, is composed mainly of yellow droplets and their cones, and is used in monocular, lateral viewing. Under exactly what circumstances the yellow area is used, or is used exclusively, is not known, but it is probably used when the bird spots an avian predator (Levi, 1974).

Rod pigment was extracted from the pigeon eye by Bridges (1962). The absorbance curve for rhodopsin agreed closely with the scotopic spectral sensitivity function function obtained psychophysically by Blough (1957). A single cone pigment, "iodopsin," was extracted from the pigeon retina by Wald (1958) and Blough's (1957) photopic function agrees well with this

pigment's absorbance function at wavelengths above 550 nm although the fit is less good at lower wavelengths.

Because of the difficulties of performing MSP, studies using other techniques, notably electroretinography (ERG), were performed to attempt to define the mechanisms of color vision. Graf and Norren (1974) measured response amplitudes at three intensities at wavelengths ranging from 400 to 700 nm. The three spectral sensitivity curves were in good agreement, although the curve obtained at the highest intensity showed loss of sensitivity relative to the other two at short wavelengths, particularly below 450 nm. This indicated the presence of a short-wavelength mechanism with a different response-intensity function than at longer wavelengths. That the increase in sensitivity at low intensity was not due to the action of rods is indicated by the fact that the stimulus beam was flickered at a frequency of 25 Hz; rods are generally not able to follow this high a temporal frequency.

At all intensities there was an increase in sensitivity below 450 nm. This the authors attributed to a spectral mechanism with $\lambda$max at 400 nm. Because a relative phase difference in ERG output between short- and long-wavelength stimuli occurred, the rise in sensitivity below 450 nm could not be attributed to a secondary peak in sensitivity of a pigment with $\lambda$max

at longer wavelengths. The phase difference in the ERG must reflect the activity of a different mechanism. The posited short-wavelength mechanism was further investigated by adapting the eye selectively to an intense yellow background. It was found that sensitivity above about 450 nm was greatly lessened, while it was largely unaffected below this value, further supporting the existence of a separate short-wavelength-sensitive mechanism, rather than the interaction of pigments sensitive to longer wavelengths.

Govardovskii and Zueva (1977) also attempted to identify multiple cone pigments. Illuminating the retina from the scleral side to avoid any possible effect of the oil droplets, they studied the early receptor potential in response to stimulus flashes of different wavelengths. They inferred at least five visual pigments: a rhodopsin with $\lambda$ max at 507 nm and cone pigments with $\lambda$ max at 562, 507, 467, and 413 nm.

Bowmaker (1977) performed microspectrophotometry on pigeon retinas and isolated three cone pigments with $\lambda$ max at 567, 514, and 460 nm. He constructed a theoretical spectral sensitivity function based on combined cone-oil droplet interactions, to be discussed below.

Table 1. Oil Droplet/Cone-Pigment Associations (Red Sector)

| Droplet | Red | C | B | Al | Ab | Clear |
|---|---|---|---|---|---|---|
| $\lambda$ T50 (nm) | 610 | 570 | 554 | 476 | 476 | ? |
| $\lambda$ max of cone (nm) | 567 | 514 | 567 | 567 | 567 | 567(?) |

From Mariani & Leure-DePree (1978).

Oil droplets. A first physical classification of the oil droplets in the pigeon was made by Bowmaker (1977). He differentiated among droplets on the basis of the wavelength at which 50% transmission occurs ($\lambda$T50). In the red field five types of droplets were found, which Bowmaker designated as B (the oil droplet of the principal member of the double cone), Clear, A, C, and Red, all found in single cones. Absorbance of the B droplet varied considerably, while $\lambda$T50's of the A,C, and Red droplets were at 473, 570, and 610 nm, respectively.

Five types of droplets were also found in the yellow field. The $\lambda$T50's of droplets in this sector were about 10 nm shorter than those in the red sector, being 470, 560, and 600 nm for A, C, and Red. For Clear droplets, absorbance rose below 425 nm. Bowmaker's oil droplet-cone relationships are shown in Table 1.

Mariani and Leure-DuPree (1978) found that oil droplets and cones could be characterized on the basis of several physical characteristics. One is oil droplet color: the authors found five types, red orange, yellow, yellow-green, and colorless. Mariani and Leure-DuPree found, as Bowmaker had not, that the accessory member of the double cone does contain an oil droplet - a colorless one.

Droplets could also be identified on the basis of their size, with red the largest and colorless the

smallest. Droplets were also classified according to retinal stratification, with the yellow droplet most vitread and the yellow-green droplet most sclerad. A review of data concerning cone-droplet associations is given in Table 2.

Oil droplet-cone pigment relationships. Mariani and Leure-DuPree (1978) classified pigeon cone and oil droplet types in the red field on the basis of their morphological characteristics. They found six different types of photoreceptor: (1) the rods, with no droplet in their inner segment; (2) the principal and (3) accessory members of the double cone; (4,5) two types of single straight cone, and (6) an oblique single cone.

Bowmaker (1977) has constructed a model of spectral sensitivity for the pigeon based on the combined $\lambda$ max's of the cone pigments and the $\lambda$T50's of the oil droplets. He stated that cutoff of the droplets will determine effective spectral sensitivity of the pigments. The effect of a pigmented droplet in any cone is to displace the maximum sensitivity of the cone to a wavelength longer than the $\lambda$max of the visual pigment, to reduce the bandwidths of the spectral sensitivity of the pigment by cutting off shorter wavelengths, and to reduce the absolute sensitivity of the cone at its $\lambda$max from that of the visual pigment unscreened by the droplet. Thus, for example, the red

Table 2. Oil Droplet-Cone Associations

| Droplet color | Red | Orange | Yellow | Yellow-Green | Colorless |
|---|---|---|---|---|---|
| Size (mμ) | 4.5 | 3.5 | 3.0 | 2.5 | 1.5 |
| λ max of cone pigment (nm) | 544Br<br>562G&Z<br>567Bo | 514Bo<br><br>413G&Z | 567Bo | 461Bo<br>467G&Z | 507G&Z<br>400G&N |
| Cone type | single straight | single straight | principal | oblique | accessory |

Adapted from Mariani & Leure Du-Pree (1978).
Br=Bridges (1962); Bo=Bowmaker (1979);
G&Z=Govardovskii & Zueva (1977); G&N=Graf & Norren (1974).

oil droplet in the red field cuts off light below about 560 nm and displaces the effective maximum sensitivity of 567 to 619 nm, reduces the absolute sensitivity at 619 nm to about 38% of the sensitivity of the visual pigment at 567 nm, and reduces bandwidth of spectral sensitivity to about 30% of that of the 567.

Bowmaker (1979), assuming linear summation of cone outputs, predicted overall spectral sensitivity by summing cone-oil droplet types in accordance with their approximate frequency of occurrence. In the red area, 80% of the cone-droplet dyads have an effective $\lambda$ max of 575 nm or above. In the yellow sector, only 12% of cone-droplet dyads measured had a $\lambda$ max exceeding 570 nm, while about 65% were maximally sensitive at around that wavelength (Table 3). All combinations of oil droplets and cone types occur in both fields, but in differing proportions. According to Bowmaker's model, the yellow field is maximally sensitive at about 560 nm; the red area is most sensitive from 580 to 600 nm (Table 4).

Bowmaker (1979) did not find a pigment with a $\lambda$ max low enough in itself to account for the birds' sensitivity to short wavelengths. He postulated that this sensitivity was due to an interaction between cones containing 567 with colorless oil droplets and 567 with A droplets. Other investigations have made an interaction of this type seem unlikely, however (see,

Table 3. Cone-Oil Droplet Combinations in the Yellow Field

| Droplet type | $\lambda$T50 (nm) | Pigment $\lambda$max(nm) | Effective $\lambda$max(nm) | % of total cones |
|---|---|---|---|---|
| Red | 600 | 567 | 613 | 12 |
| C | 562 | 514 | 567 | 12 |
| B | 499 | 567 | 567 | 51 |
| Ared | 470 | 567 | 567 | |
| Agreen | 470 | 514 | 525 | 25 |
| Clear | ? | ? | ? | |

From Bowmaker (1979).

Table 4. Cone-Oil Droplet Combinations in the Red Field

| Droplet type | λT50 (nm) | Pigment λ max(nm) | Effective λ max(nm) | % of total cones |
|---|---|---|---|---|
| Red | 610 | 567 | 619 | 23 |
| C | 570 | 567 | 575 | 27 |
| B | 522 | 567 | 570 | |
| 554 | 567 | 589 | 30 | |
| Ared | 476 | 567 | 567 | |
| Ablue | 476 | 460 | 485 | 20 |
| Clear | ? | 567(?) | 567(?) | |

From Bowmaker (1979).

for example, Graf, 1979, discussed below).

A recent study by Wortel, Wubbels, and Nuboer (1984) measured the photopic spectral sensitivity of the red and yellow fields electrophysiologically in two ways; using a minimum-amplitude ERG response to flicker photometry and an increment threshold using a criterion response. Birds were placed in such a way that either the red or yellow field was stimulated exclusively. The investigators found that between 450 and 550 nm the yellow field is up to .8 log units more sensitive than the red field. Below 470 nm sensitivity measured by the contrast sensitivity technique was much greater than for flicker photometry. The authors speculate that the postulated violet-sensitive cone system has a slower response time than the other color mechanisms, and would be unable to follow high stimulus frequencies; thus violet cones will only have small amplitude ERG responses to flickering stimuli. Violet sensitivity, they assert, is probably mediated by short-wavelength cones (the 413 nm of Govardovskii and Zueva, 1977) with clear droplets. Still unclear is the source of sensitivity to even shorter wavelengths.

## Function of the Oil Droplets

Although there is a growing amount of information about physical properties of the cone pigments and oil droplets, and their transmission and absorbance properties, there is still no general agreement on the function of the droplets. A number of hypotheses have been advanced, not all of them mutually exclusive. King-Smith (1969), at a time when only a single cone pigment had been identified in the pigeon, proposed that oil droplets interacted with this single pigment to provide a mechanism for color vision. Other investigators suggested that while color vision is not wholly dependent on the droplets, they do mediate detection of color differences by producing narrow-band sensitivity channels for color discrimination, thus sharpening discrimination ability (Delius, Thompson, Allen, & Emmerton, 1972; Martin & Muntz, 1979).

Some researchers (e.g. Hailman, 1964) have attempted to relate oil droplet transmission characteristics to color vision preferences in newly hatched birds. Hailman noted that gull chicks (Larus atricilla) peck at their parents' red beaks, which elicits regurgitation by the parent. He found that gulls responded preferentially to red and blue light over green and yellow. Hailman suggested that the gulls' red and yellow oil droplets interacted with a single

cone pigment to produce a transmission spectrum of oil droplets virtually identical with pecking rate to various spectral stimuli. Theories that rest on a single pigment type, however, are not likely to be tenable, since it is now known that there are multiple cone pigments. Also, as Wallman (1979) noted, theories that attempt to explain color preference on the basis of oil droplet characteristics have difficulty explaining the great variability within and between species in color preference, since oil droplet types are so similar in (diurnal) birds.

In another such study, Mayr (1972) examined various species of the family Ploceidae, to test whether variation in oil droplet coloration was equated with plumage coloration. Mayr's study was prompted by findings of Peiponen (1963), who suggested that birds with blue plumage should have fewer red and yellow droplets than birds with other colored feathers; because of this difference in oil droplet pigmentation, they should be better adapted to recognize conspecifics. Mayr concluded that although there were small differences in the proportion of red droplets present for the various species, these were insufficient to account for species-specific plumage recognition.

Kirschfield (1982) suggested that the droplets protect against photooxidation in the eyes and

photoreceptors. Since the mitochondria of receptors contain other pigments, these might become photooxidized, particularly by shortwave and ultraviolet light. In mammals, this unwanted short-wavelength light is filtered out by pigments in the lens and macula. Birds' eyes do not have these pigments. The droplets may protect receptors from photooxidation from excess light at the short end of the spectrum. As the author notes, however, this theory does not explain how receptors containing colorless droplets escape injury.

Young and Martin (1984) proposed that among other functions droplets serve as microlenses with a light-gathering function. They noted that increased photon capture would result in improvement in sensitivity, contrast detection, and motion detection. This explanation would extend to the colorless oil droplets found in nocturnal birds, as well as reptiles, amphibians, and marsupials.

Wohlbarsht (1976) suggested a role for the oil droplets based on the chemical properties of the cone pigments and the filter properties of the ocular media. When the all-*trans* molecule of the chromophore of the visual pigment is isomerized to the 11-*cis* form, a second absorption band appears in addition to the primary absorption band. For rhodopsin, for example, the fundamental peak is at 500 nm and the *cis* peak is

at 340 nm. Cone pigments have a wide range of absorption peaks - a few in blue, the rest in green, yellow, and red. It is now known that the cis peak does affect the visual system and can produce both visual excitation and bleaching of pigments. If the oil droplets serve as band-pass filters to exclude short-wavelength light, then this filtering action could result in greater spectral purity for each of the cone pigments. Wohlbarsht suggested another function for the oil droplets: to correct for chromatic aberration. If the eye is focused for light at the yellow or red end of the spectrum, blue light will form an out-of-focus blue image. In birds it may be that the oil droplets filter the stimulus. This function is assumed in primates by a yellow macular and lens pigment, but these pigments are absent in birds.

## Behavioral studies of oil droplet functions.

As noted previously (Dücker & Tiemann, 1972), the young of the common lizard L. vivipara and the blindworm A. fragilis are born with oil droplets less pigmented than those of adults of those species. Thus if differences in color vision appeared between adult and young, one might infer a role for the droplets in color vision. An optomotor drum with stripes of yellow,

red, blue, and green of 16 different intensities was used. As indicated by the optokinetic response, all ages of L. vivipara could differentiate yellow, red, blue, and green, regardless of intensity. The one-day-old young of A. fragilis distinguished yellow and red. They appeared to be blue-green colorblind, which is also true of adults of this species. The authors concluded that color vision capability is not decisively influenced by postnatal pigmentation of the oil droplets. The satisfactoriness of this conclusion will be discussed after some studies of the Japanese quail have been reviewed.

Several behavioral studies have been conducted in which quail were fed a carotenoid-free diet. It is possible, by rearing birds on a diet without carotenoids, to produce birds with unpigmented droplets. The birds' visual behavior was tested to clarify the role of the droplets. One such study was done by Wallman (1979). To test for color blindness in birds raised on a carotenoid-free diet, the bird's optomoter response was measured. The optomotor response will occur whether the stripes contrast in brightness or hue. Thus in a cylinder made up of alternating red and green stripes of equal brightness, an animal with color vision will respond, whereas a colorblind animal will not. To make the test optimally sensitive, luminance of the red and green stripes must

be varied. In a nearly colorblind animal the apparent contrast of the stripes is almost completely dependent on the luminance ratio of the stripes. Responding in a normal bird would be less affected by changes in red-green luminance, since the animal would always see the chromatic contrast. The apparent contrast of the stripes was measured by imposing colored stripes on another, achromatic grating moving in the opposite direction. The bird followed whichever grating had larger contrast. Normal birds responded mainly to color contrast, while carotenoid-deprived birds responded mainly to brightness contrast. Wallman concluded that oil droplets are not essential for color vision, but that in their absence color vision deteriorated. That this deficit is likely due to the depletion of the droplet pigment is shown by the fact that deprived birds fed on a carotenoid-enriched diet so that their droplets became pigmented showed an optomotor response akin to that of normal birds.

Kovach, Wilson, and O'Connor (1976) tried to determine whether the pigmented oil droplets were the morphological basis of color preference in quail selected for red or blue preference. Birds were compared according to genetic lines of origin and presence or absence of oil droplet pigments. Very large numbers of birds were tested in a pyramid-shaped apparatus. In each compartment of the pyramid were a

pair of visual stimuli: a red or blue one-inch square stimulus patch produced by gelatin filters. What the measure of preference was is not clear. Apparently approach to one or the other of the colored stimuli opened a trap door, dropping the bird to a compartment on a lower level, of which there were eight. Position on each row depended on prior choices, and arrival in the collection box on the bottom row indicated the number of choices made to each stimulus on prior trials. One might reasonably suppose that being dropped through a trapdoor is an aversive experience; the effect of such a stimulus on future choices between the color stimuli seems not to have been considered. Carotenoid deprivation resulted in a shift toward red preference in both genetic lines, but the magnitude of difference between mean performances of the two genetic lines remained the same as the differences between the corresponding genetic lines reared on a normal diet. This indicated that the oil droplet pigment was not the structural target of genetic selection for color preference. To ascertain that choice was not based on intensity differences between the two stimuli, the authors varied their intensity. Large changes in preference for blue with an increase in intensity resulted, but no such change for red was found. Thus preference for red was presumed to be based only on hue properties of the stimulus.

Since Wallman's (1979) study indicated that birds with pigment-free droplets became relatively more sensitive to intensity, it was necessary that the stimuli in the Kovach, Wilson, and O'Connor study be effectively equated for brightness. The visual stimuli are not described in the article, but in an earlier article (Kovach, 1974) the intensity manipulations were as follows: red and blue stimuli were first equated on the basis of physical intensity; they were then lowered by 50% from this value, and finally they were equated for human photopic luminosity. This inadequate control procedure makes it difficult to conclude that the birds were not using intensity properties of the stimuli to discriminate between them. Since the oil droplets act to cut off light at short wavelengths, the increase in preference for (salience of) the blue stimulus with increasing intensity in birds with colorless droplets may mean that these birds were less able to distinguish between red and blue.

Kovach, Wilson, and O'Connor concluded that "the totality of data does not lend support to earlier interpretations that retinal oil droplets are involved in color discrimination (p. 1150), an assertion that will be considered further below.

Dücker and Schulze (1977) also reared quail with colorless droplets and tested their ability to distinguish between monochromatic red, green, blue, and

yellow stimuli and a white light of varied intensity. A large range of intensities of the white light was used for each of the monochromatic stimuli, and it seems likely that a brightness match was achieved. Birds were required to choose the colored stimulus in each white-color pair. Quail with unpigmented droplets were able to perform this task and the authors concluded, as did Kovach, Wilson, and O'Connor, that the oil droplets are not necessary for color vision.

Since it has been demonstrated that diurnal birds have more than a single cone pigment, one would not expect color vision to be totally dependent on the pigmented oil droplets. Primates, obviously, discriminate color without oil droplets, using only cone pigments. It is more likely that the droplets sharpen color discrimination, especially at longer wavelengths. Little is known about the spectral sensitivity or wavelength discrimination ability of normal lizards or Japanese quail. Therefore it is impossible to conclude that because the animals are able to make crude discriminations between monochromatic and white stimuli, or between colored stimuli imperfectly matched for intensity, or even between colors appropriately matched for intensity, the oil droplets are not necessary for normal color vision. It is entirely possible that a very specific but significant ability to distinguish small differences in

wavelengths depends on the presence of pigmented oil droplets. Such a dependency would not be detected by the crude discrimnations required in the Dücker and Tiemann (1972), Kovach, Wilson, and O'Connor (1976), and Dücker and Schulze (1977) studies described above.

## Behavioral Studies of Color Vision in the Pigeon

It would be desirable, therefore, to explore the role of the oil droplets in a species for which there is more complete and precise information about color vision capabilities. Such information is abundantly available for the pigeon.

The first behavioral study on color vision in the pigeon was done by Hamilton and Coleman (1933); although peculiarities of method make its conclusions questionable, it is perhaps worth noting that these investigators found, as have all later ones, that hue discrimination is best at around 600 nm.

A study by Wright and Cumming (1971) employed a matching-to-sample procedure to construct a color-naming function for the pigeon. The birds were first trained to peck a display key illuminated by monochromatic light of 512, 572, or 655 nm and then to peck the side key lit with light of the same wavelength. During testing, new probe wavelengths were

presented on the display key and the proportion of side-key pecks to each of the training wavelengths was measured. The resulting color-naming function divided the spectrum into a region below 540 nm, a region between 540 and 595 nm, and a region above 595 nm. The crossover wavelengths at the color boundaries (540 and 595 nm) remained constant even when the test stimuli were changed to 473, 555, and 633 nm. When the boundary wavelengths themselves were used as color names, acquisition of matching-to-sample slowed and the color-naming data became extremely variable: evidently the transitional hues were difficult for the birds to categorize. Wright and Cumming (1971) concluded that pigeons categorized colors differently than humans do: the pigeon 540-nm transition occurred in the middle of human green, and the 595-nm transition point does not coincide with the human yellow-red transition. The pigeon seems to experience short- and long-wavelength stimuli as being similar to each other, as do humans.

Schneider (1972) constructed a color circle for the pigeon. (For humans, this geometric device is a useful representation of color perception, with long and short wavelengths appearing similar.) The distance between points in space represents the extent of the perceived dissimilarity between colors. A yes-no signal detection procedure was used to measure dissimilarity of pairs of monochromatic stimuli. The birds compared

all possible pair combinations of 12 wavelengths between 454 and 670 nm. A statistical technique of multidimensional scaling was then used to generate the color circle, in which distance between any two loci is proportional to the distinguishability of the respective wavelength. Schneider found, as did Wright and Cumming, that long and short wavelengths resemble each other. The most dissimilar regions - where wavelength discrimination is best - fall at about 500, 540, and 600 nm.

Wright (1972) used a two-alternative forced-choice procedure to investigate wavelength discrimination. He found that there was a nearly linear relationship between sensitivity ($d'$) and wavenumber difference. Minima occurred at 600 nm, and at 540-550 nm and 500 nm, suggesting to Wright tetrachromacy within the spectral range of 470-660 nm. Two of these minima (545 and 600 nm) are consistent with the crossover points denoting color boundaries found by Wright and Cumming (1971).

In humans, wavelength discrimination and generalization studies show the following relationship: generalization gradients are steeper in spectral regions where best discrimination occurs (e.g., Kalish 1958). This relationship was not found in the classic Guttman and Kalish (1956) study of wavelength generalization in the pigeon. Instead of assuming that

generalization-discriminability relationships are different in the pigeon than in humans, P. Blough (1972) hypothesized that certain variables that were not controlled in the earlier study may have affected performance. Specifically, the effects of intensity were not controlled for in the Guttman and Kalish study. In her study, Blough used D. Blough's (1957) data on pigeon photopic sensitivity to adjust the intensities of the various monochromatic stimuli. Also, she examined the effects of different levels of intensity, and, finally, used a maintained discrimination method rather than collecting data during extinction. She first used the extinction procedure to gather baseline data. She found that generalization gradients were very broad. Gradients around 540 and 570 nm were relatively flat, while response probablility fell off rapidly above 630 nm. (She points out that this might support the Wright and Cumming finding of a 600-nm boundary. In the P. Blough study, the gradient comes to a peak at 600 nm and falls off symmetrically on both sides. Her data do not give evidence of a boundary at 540 nm, however - the gradient is flat at 540 nm and the 570-nm gradient does not fall off in that direction.)

When a maintained discrimination method was used, that is, when responding was maintained by infrequent primary reinforcement, gradients were more consistent,

and steeper. Blough attribued this to the larger response sample made possible by continuing reinforcement. The steepest gradient was at 600 nm, while at 540, 510, and 570 nm gradients were flatter but symmetrical; at the spectral extremes, gradients were aymmetrical with responding falling off at the extreme high or low end. These data do support Wright and Cumming's (1971) findings of color boundaries at 600 and 540 nm.

Jitsumori (1978) attempted to explain the differences between Wright's (1972) and Blough's (1972) data below 600 nm by using a combination of the two techniques: using the yes-no response paradigm of Wright and the discrimination-generalization technique used by Blough. Like all other investigators, she found a minimum at 600 nm, conflicting results in the middle of the spectrum, and a minimum at 450 nm, at a wavelength below that studied by Blough and Wright.

Graf (1979) reported a series of experiments designed to provide information about underlying spectral mechanisms. Behavioral spectral sensitivity was measured by determining the pigeon's increment threshold for small chromatic stimuli superimposed on large backgrounds of either white, red, yellow, or blue. A go/no go procedure was used, with background alone serving as S+ and stimulus superimposed on background as S-. Training continued until 90% correct

responding was reached. During testing, 120 trials were run, half with background, half without. Twenty percent of the background-plus-stimulus trials were presented with the test spot radiance set at the same level used in training. The remaining 80% of trials used lower radiances: 20% were attenuated by .2 log unit, 20% by .4, 20% by .6, and 20% by .8 log unit. For the white background there appeared to be four peaks of sensitivity, at 400-420 nm, at 480 nm, at 550 and at 615 nm. There was a deep trough at 450 nm. For the red background there were peaks at 400, 480, and 570 nm, with a trough at 450 nm. For the yellow background there were peaks at 400-420, 480, 540-570, and 615 nm and a trough at 450 nm. Two levels of blue background were used. At the less intense one there were peaks at 400, 540-570, and 615 nm; for the more intense background only two peaks were seen, at 540-570 nm and at about 620 nm. These data support the hypothesis that there are at least four mechanisms contributing to spectral sensitivity. Sensitivity at short wavelengths seemed likely to be due to a short-wavelength pigment rather than to an interaction between mechanisms sensitive to longer wavelengths. Evidence for this comes from the fact that sensitivity to short wavelengths disappears in the presence of a short-wavelength background.

A few studies have attempted to study behaviorally

differences in spectral sensitivity between the red and yellow fields. The most obvious difficulty in this kind of study is delivering the stimulus in such a way that one can have confidence that it is falling in one or the other retinal area. P. Blough (1979) attempted to overcome this difficulty by using a brief (200-400 msec) stimulus flash and a small (3-mm diameter) stimulus area. The flash was produced by a key peck so the bird's head was always in the same position at the time of stimulus presentation. The stimulus was positioned either frontally (for red field stimulation) or laterally and slightly superior (for yellow field stimulation). The author used a threshold procedure to assess sensitivity. Birds pecked at the upper of two keys until a flash occurred; after the flash, a peck to the lower key was occasionally reinforced. Wavelengths of 525, 575, and 625 nm were used since electroretinographic studies (King-Smith, in Muntz, 1972) suggested that the red field is less sensitive than the yellow between 500 and 600 nm. Blough did not find behavioral evidence for this, however; in no case was sensitivity higher when the stimulus was viewed laterally than when it was viewed frontally. Blough noted, however, that it was not possible to be sure that the red or yellow field was exclusively stimulated; perhaps the relatively poor overall performance when the stimulus was presented laterally

and superiorly was due to the novelty and awkwardness of that stimulus locus.

Romeskie and Yager (1976) did a psychophysical study of photopic spectral sensitivity, using a two-key forced choice method. A monochromatic stimulus presentation was altered randomly between two keys. A peck at the light was reinforced; a peck at the blank key resulted in time out. When criterion responding was reached at one stimulus intensity level, the intensity of the stimulus was lowered by .3 log unit until threshold was reached. Romeskie and Yager found that the peaks and minima of sensitivity to red and yellow light occurred at longer wavelengths than in D. Blough's (1957) study. Romeskie and Yager reported a more rapid loss of sensitivity toward the middle of the spectrum and a faster rise at short wavelengths. They suggested that the differences in shape of the two luminosity curves reflected the differences in retinal area stimulated. Their study used the same key for stimulus and response, while in Blough's study the response key was situated below the stimulus key. Thus, Romeskie and Yager argued, in Blough's study the stimulus fell on the yellow field, while in theirs the red field was stimulated. It is just as difficult with this study as with P. Blough's study, however, to be sure of where the stimulus in fact was falling. Perhaps it would be useful at this point to review

available information about the pigeon's fields of view and their consequences for vision research.

## Pigeon Fields of View

Because the eyes are set laterally, birds have two fields of view; a lateral, monocular line of sight, and a frontal, binocular one. It has long been asserted that these two different fields have different properties, namely that the frontal binocular field is myopic, while the lateral monocular field is emmetropic or hyperopic. The observations of pigeon breeders and fanciers, for instance, led to this conclusion: "The vision of the pigeon is of two types: for distant objects only one eye is used (monocular vision), while for grain or other close objects both eyes are used, looking forward (binocular vision)" (Levi, 1974, p. 378). The acuity of this lateral vision was also assserted: "The ability of a pigeon, confined to a pen for many prior generations, to distinguish the difference between a hawk and a turkey vulture or black vulture at a great height is astounding" (Levi, 1974, p. 378).

In 1964 Catania noted that evidence for a myopic anterior field came from pigeon research using operant techniques, which often require a key peck directly in

front of the bird's beak. If the frontal viewing field were not myopic, presumably stimulus control could not be achieved. Catania used this information, as well as structural and optical properties of the pigeon eye, to construct a model of the visual system that supports theories of frontal myopia and lateral hyperopia.

Because of the very different properties of the two fields, it is obviously important for an experimenter to know where on the retina a stimulus falls. A recent experiment by Goodale (1983) attempted to establish that the stimulus in the typical experimental situation - a key placed anteriorly at eye level and at a short distance from the eye - falls on the so-called red field. Pigeons were trained in a "feature-positive discrimination" in which a positive stimulus had a single distinctive feature, in this case a 2-mm black dot projected onto a key. If a bird pecked the key when the positive stimulus was presented it was reinforced; if the key was pecked during the negative stimulus a 30-sec time out ensued. Pigeons easily learned the task, and they were then filmed to look for characteristic head movements during the moments prior to the key peck. These films allowed estimates to be made of where on the retina the stimulus fell. Goodale found that on both positive and negative trials the birds made several head fixations, each preceded by a rapid, saccade-like movement of the head. The last two

movements before the peck had considerable intertrial consistency for all birds. Goodale estimated the distance between the center of the key and the center of the eye nearest the key for these two fixations and found that the mean distance for all birds for positive trials was 81.7 mm for the penultimate and 54.5 for the final fixation. Goodale also calculated viewing angles for the two fixation points and found that these angles placed the positive stimulus well within the binocular field and within the red area of the upper dorsal quadrant.

Several experimenters have tried to test the hypothesis that the pigeon is frontally myopic and laterally hyperopic. In P. Blough's (1979) experiment the pigeon's task was to enter one of two alleys. At the end of one was a blank target; at the end of the other was a striped target of variable spatial frequency. Location of the targets varied randomly. By varying length of the alley, target distances could be manipulated. Acuity was assessed at distances varying from 10 to 75 cm for both free-viewing and frontal fields (in the latter case the bird wore goggles, allowing only frontal viewing). The relationship between acuity and target distance for frontal viewing was different than for free viewing; acuity improved with distance when free viewing was allowed, and little or no improvement in acuity with

distance was found when only frontal vision was used, suggesting that in the free-viewing condition the lateral, farsighted field was used.

More recently, Bloch and Martinoya (1982) compared the acuity of the two retinal areas of higher cellular density, the area dorsalis in the red field and the central fovea in the yellow field. They used a variable ratio pecking schedule and tachistoscopic (300 msec) presentation of the stimulus following a peck to the display key, the latter to ensure that a head or eye movement could not be initiated during the stimulus presentation. Birds had to distinguish the orientation of square-wave gratings of increasing spatial frequency (1-5 cycles/degree). Stimuli were 22° below the beak for frontal and 80° back from the beak for the lateral field, and were presented at 10, 20, 40, and 80 cm distance for each. Frontal acuity decreased with distance while lateral acuity increased.

Finally, Martin and Muntz (1979) used an ingenious procedure to restrict the stimulus to either the red or yellow field. Pigeons were trained to peck in response to a light stimulus presented at fixed loci inside a dome-shaped headgear bolted to the skull. Stimuli were delivered to the dome through fiber optic light guides in order that they might fall in either the red or yellow field. A two-choice discrete-trials simultaneous-discrimination procedure was used:

subjects were trained to respond to one of the keys when the stimulus light was presented and to the other in the absence of light. Sensitivities to monochromatic stimuli of different wavelengths were determined by constructing psychophysical functions. Clear differences were evident between the two spectral sensitivity functions: red-field functions were narrower than yellow, while the yellow field was more sensitive than the red at wavelengths below 550 nm; the two fields show similar sensitivity above 600 nm.

Although these findings agree with the electrophysiological data (King-Smith in Muntz, 1972; Wortel, Wubbels, & Nuboer, 1984), the study depends for its validity on the assumption that pigeon eye movements are so restricted that an eye movement could not shift the stimulus into the other field. This has generally been thought to be the case, for two reasons. First, birds appear to make saccade-like head movements in scanning a visual field. Secondly, the shape of the avian eyeball greatly restricts the degree to which it can move around in its socket. A recent study by Bloch, Martinoya, and Riveau (1981), however, suggests that pigeon eye movements are great enough to displace the stimulus from one visual field to another in the Martin and Muntz (1979) paradigm. The investigators recorded the electrooculogram of the horizontal component of eye movements, and they found that eye

movements were mostly saccadic and could attain about $15^{\circ}$ from the resting position. The pattern of movement suggested that these eye movements contributed both to binocular fixation and to monocular orientation and pursuit.

## Wavelength-Intensity Interactions

Because perception of color is based not only on hue, but on brightness and saturation as well, considerable care must be taken to ensure that a discrimination intended to be made on the basis of wavelength alone is not also influenced by other stimulus properties. Stimuli of different wavelengths must be matched for intensity in accordance with the appropriate spectral sensitivity function of the subject, and the intensity of the comparison stimulus should be varied randomly around the presumed point of subjective equality to further ensure that discrimination is based on wavelength alone.

If animals are presented with information about both intensity and wavelength a number of questions arise. For instance, if a bird is asked to discriminate color, and is given differences in both wavelength and intensity on which to base his decision, which information will be most readily utilized? How does

this compare with the behavior of other species? Do other animals with color vision find wavelength a more salient stimulus characteristic than intensity? Is there any relationship between threshold for intensity and wavelength? Specifically, do pigeons use intensity information more at spectral loci where wavelength discrimination is relatively poor than at areas of best discrimination?

Intensity-wavelength interactions in animals other than the pigeon. The question of relative salience of intensity and wavelength has been asked with a number of species. In the cat, the nature of color vision has long been something of a puzzle. While electrophysiological data showed that the cat's visual system responded differentially to wavelength, behavioral studies had not shown much evidence of color vision (Mello & Peterson, 1964). Mello and Peterson introduced operant techniques into the study of cat color vision: using a differential reinforcement schedule responses to red were reinforced, while those to green, blue, and yellow were not. The intensity of each stimulus was varied over a wide range; it was found that cats could learn these wavelength discriminations even when stimuli were matched for intensity.

In a later study, Mello (1968) specifcally compared attention to intensity versus wavelength. Cats first

learned an intensity discrimination; a generalization test indicated that they were responding to intensity. The cats then learned a color discrimination. When, in a generalization test, the stimuli were equated for physical intensity, most cats did not give evidence that they were responding to wavelength, responding maximally to another wavelength or not consistently to any. When the wavelengths were not matched for intensity the cats showed a generalization gradient with a peak at longer wavelengths. These longer-wavelength stimuli were more intense than the training stimulus. Generalization gradients to wavelengths of unequal intensities seemed to be based on the dimension of relative brightness (based on electrophysiological data on photopic spectral sensitivity) rather than on physical intensity. The cats finally did learn a differential wavelength discrimination task, but, as Mello noted, until they were trained specifically to discriminate between two wavelengths, color appeared to be an irrelevant dimension in comparison with intensity.

Clayton and Kamback (1966) extended Mello's findings by using additional wavelengths. An achromatic stimulus was tested against blue, green, yellow, and red stimuli, and all possible color combinations except blue and red were compared. Two cats were used; at least one cat could make all discriminations except

yellow versus greeen and yellow versus red.

Brown, Shively, LaMotte, and Sechzer (1973) found a similar inability to discriminate between yellow and green, or between either yellow or green and white and suggested that possibly the spectral region between 520 and 570 nm is indiscriminable for the cat.

Loop and Bruce (1978) suggested that stimulus size is a critical variable in cat wavelength discrimination. Four cats learned a brightness discrimination on a blue background, followed by a wavelength discrimination between blue and green. The animals had learned the brightness discrimination with little difficulty, but were unable to perform the wavelength discrimination at better than 65% to 70% accuracy. Performance was unaffected by changes in intensity or contrast, but discrimination improved greatly when stimulus size was increased from 4.5 to 32.5 $cm^2$. At stimulus sizes less than 32.5 $cm^2$ performance deteriorated, reaching chance at .36 $cm^2$. Stimulus size did not affect the intensity discrimination, however. This study also suggested at least a partial explanation of contradictory prior findings: in those studies where visual angle subtended was large, wavelength discrimination was demonstrated.

Brightness control procedures in these experiments appear to have been impeccable. In general, the authors conclude that the cat does have some color

vision capability, especially at shorter and longer wavelengths, but that other parameters, notably stimulus size and intensity, readily interact with wavelength discrimination.

The color vision capabilities of ground squirrels, the sciurids, are of interest because their retinas are so dominated by cones. The photoreceptor population is about 90% cones (Jacobs, 1978). If these cones contain different kinds of photopigment, the animals should be capable of at least some degree of wavelength discrimination. For the prairie dog Jacobs and Pulliam (1973) first obtained a spectral sensitivity function that showed at low luminance a peak at 520-540 nm, with a sharp falloff on both sides; at higher luminance the peak shifted to slightly higher wavelengths with a less abrupt loss of sensitivity at spectral extremes. The animals could learn discriminations between 460 or 560 nm and white light, but there was a small spectral neutral point at about 500 nm, suggesting that the prairie dogs are dichromats. In a test for intensity versus color discrimination if stimuli were matched for intensity, the animals were unable to detect a difference between 580 and 612 nm, but if a .5-log unit intensity difference was added to the wavelength difference, the discrimination could be learned.

In a comparative study of color vision of five species of sciurids, Jacobs (1978) found in the

golden-mantled ground squirrel a low-luminance spectral sensitivity peak at 500-540 nm; at higher luminances there was a bimodal peak at 450 nm and at 520-560 nm, with a trough at 500 nm. Jacobs noted that the animals evidently discriminated wavelength less well than intensity, judged both by length of time required to learn and by the accuracy of performance at asymptote. They discriminated between 460 or 560 nm and white; a spectral neutral point appeared at about 507 nm. Jacobs repeated these experiments with Mexican, thirteen-lined, and California ground squirrels; data had previously been obtained from the prairie dog. For all of these species, spectral sensitivity at low and high luminances was virtually identical, and all showed an inability to discriminate monochromatic from white light at around 505 nm.

The work with cats and ground squirrels suggested that these animals can make at least some color discriminations, but they more readily attend to other stimulus properties, notably intensity. The question arises whether animals more sensitive to wavelength differences are less sensitive to intensity differences.

Most of the work done on apes and old-world monkeys suggests that these species have spectral sensitivity and color vision abilities virtually indistinguishable from those of humans (Sidley & Sperling, 1967;

Sperling, Sidley, Dockens, & Jolliffe, 1968; DeValois & Jacobs, 1971; DeValois, Morgan, Polson, Mead, & Hull, 1974; Jacobs, 1981). Most of the work has been done with various species of macaque. Sidley and Sperling (1967) obtained a spectral sensitivity function from the rhesus monkey, showing peaks at 590-610 nm, 530 nm, and 430-450 nm. There were troughs in the function at 480 and 580 nm, and sensitivity fell off rapidly above 640 nm.

DeValois, et al. (1974) tested three species of macaque (Macaca nemestrina, M. fascicularis, and M. speciosa) on a variety of color vision tasks: a flicker-frequency/intensity function, a Purkinje shift experiment, a wavelength-discrimination experiment, an anomaloscope test, and a saturation discrimination experiment. All of these tests yielded functions practically identical to those for humans.

In an experiment that explicitly tested the primacy of the two variables, Humphrey (1971) compared color and brightness preferences in Macaca mulatta. The dependent variable was length of time a stimulus was chosen to be viewed - a measure of preference. Four monkeys revealed a brightness preference monotonically related to intensity over the range of stimuli used. When preference for various colored lights versus white lights of matched intensity was investigated, it was found that all subjects preferred blue and green to

white but preferred white to yellow, orange, or red. For all subjects color preference was monotonically related to wavelength, with blue most and red least preferred. This uniformity of preference disappeared when complex stimuli (colored slides) were used.

For some time the status of color vision in the new world species of monkeys tested was uncertain. The consensus until recently appeared to be that these animals, while they have color vision, have color capability very different from that of man or the old world monkey. Jacobs (1963) and DeValois and Morgan (1974) tentatively concluded from hue discrimination and neutral-point experiments that squirrel monkeys are protanomalous trichromats. More recently, work by Jacobs has suggested that there are some six distinct types of color vision in the squirrel monkey (Jacobs, 1983; 1984). Ten animals were run on wavelength discrimination and Rayleigh matching tasks. The discrimination functions showed two general patterns: one, produced by four subjects, showed minima at 490 and 585 nm, with poor discrimination in between and at the extremes. The other pattern showed a minimum at about 500 nm, and rapid falloff of discrimination above that wavelength. The human wavelength discrimination function is similar in shape to that of the first group of monkeys, although humans have greater sensitivity at all wavelengths. Intensity discrimination appears to

be similar for humans and these monkeys. These animals showed no neutral point, and are classified as trichromats. The second group showed a neutral point at about 484-500 nm. Not only are some monkeys trichromats and some dichromats; there are large variations within these two classifications. These resolve themselves into three subcategories for each larger category. There are thus three types of dichromacy: protanopia, deuteranopia, and a deficit unique to the species. The trichromatic group displayed protanomaly, deuteranomaly, or normal trichromacy similar to that of humans.

It seems then, that many species are extremely sensitive to the intensity content of a color stimulus, so much so, that even very small brightness cues may cause an animal to ignore wavelength cues. "In testing large numbers of subjects from various mammalian species, some of which have 'good' color vision, I have often observed that given a luminance difference as a cue, the animal frequently uses that as a basis for discrimination, even if a color difference known to be discriminable is available" (Jacobs, 1981, p. 169).

Intensity-wavelength interactions in humans. Wavelength and intensity studies have also been carried out on human infants. The general conclusion seems to be (Werner & Wooten, 1979) that by two months infants are at least dichromats and that cone pigments may be

anomalous. There is no clear evidence that young infants are trichromats. Color vision may have attained its adult trichromatic form by four months. Doris, Casper, and Poresky (1967) measured brightness thresholds in infants at two different ages: 1-4 days and 45-113 days. The researchers found that the groups showed Weber fractions of .5 and .26 respectively, suggesting a rapid development of brightness discrimination. Schaller (1975) studied interaction of brightness and hue. He taught infants aged 2.5 to 2.75 months a red-green hue discrimination, using looking time as a dependent variable. The intensity of the two stimuli was varied over a 2.25-log-unit range. He found that infants responded both to the reinforced hue and to intensity: infants looked longer at the reinfored hue and at the bright conditions of the unreinforced hue.

Given considerable evidence of infants' sensitivity to luminance cues, Peeples and Teller (1975) did a brightness difference threshold test preparatory to doing a color-discrimination task, to determine what increment size would be appropriate as a control in a color discrimination task. Two-month-old infants were presented with bars of white light superimposed on a white screen. The intensity of the bars could be varied. If intensity varied from that of the screen the infants fixated the bars. An observer placed

behind the screen judged from the infant's fixation point which bars differed in intensity from the background on each trial. It was found that infants could discriminate perfectly at .1-log-unit difference, performed at a rate of about 65% correct at .08 log unit, and performance fell to chance at .02 log unit. This finding prompted Peeples and Teller to use an intensity increment of .085 log unit for a red-white discrimination test. Infants could discriminate red from white at all intensities.

Human adults are much more influenced by the chromatic than the luminance component of a colored stimulus. Evidence of this comes from heterochromatic matching studies (Cornsweet, 1970). Human adults find it very difficult to match intensity of two patches of light if the hue is different, and if a number of comparisons of the same stimuli are collected, it will be found that variability is large. Humans can easily make hue matches, even if the stimuli differ in intensity, and variability will be very low. "When two patches are different in wavelength, equal brightness settings are very unreliable, whereas when they are different in intensity, equal hue settings are highly reliable. To put it very generally: it is extremely hard to judge the relative brightnesses of different hues, but it is easy to judge hue, regardless of brightness" (Cornsweet, 1970, p. 235).

It has generally been found that a small luminance contrast improves hue discrimination. Hilz, Huppman, and Cavonius (1974) tested this finding by asking subjects to make a hue discrimination between adjacent bars of a square-wave grating when these bars were matched for luminance and when there was a .045-log-unit difference between adjacent bars. It was found that the shape of the wavelength discrimination function was not affected by luminance (or by cycles/degree) but that threshold was higher if luminance contrast was absent.

A study by Kerr (1974) attempted to tease out the relationship between chromatic and achromatic channels. He noted that opponent process theory predicts that brightness contrast produced by a chromatic inducing field will be related only to its own brightness and will not be affected by the wavelength composition of either inducing field or reacting field, except as wavelength affects luminance. There is evidence for and against this prediction. The Kerr study predicted that if chromatic mechanisms are active at threshold, then just-detectable stimuli should convey information about wavelength. Also, the influence of monochromatic annuli on test stimuli should be the same for detection and identification. The study examined the effects of annuli of different wavelength on detection of monochromatic stimuli on an achromatic background.

Five different annulus conditions were used: none, 666 nm, 466 nm, 533 nm, and achromatic. Kerr found that the effect of annuli on detection of the monochromatic stimuli is selective: long-wavelength annuli inhibit detection of long-wavelength stimuli and short-wavelength annuli inhibit detection of short-wavelength stimuli. A second part of the study examined whether just-detectable stimuli could be identified on the basis of wavelength, and if so, whether the effects of the annuli on any given discrimination would also be wavelength specific. He found that the presence of any annulus, especially a chromatic one, reduced the effect of stimulus intensity. Subjects could discriminate among stimuli at all intensity levels. Results indicate that subjects are able to report chromatic aspects of just-detectable monochromatic stimuli when these stimuli are presented on a photopic achromatic background. Also, when the effects of different annuli on thresholds for various monochromatic stimuli are compensated for, there is no differential effect of chromatic annuli on discriminability of test stimuli. The annuli reduced differences in stimulus discriminability among four intensity levels, but the effect was not wavelength specific. This indicates that chromatic mechanisms are active at threshold levels.

In a later study, Kerr (1976) speculated that differing results in experiments investigating wavelength-intensity interactions may be the result of different methods used. The Kerr study compared effects of simultaneous contrast on flicker photometry and direct brightness matching. To the extent that chromatic activity contributes to stimulus brightness, relationships between wavelengths of test and annulus would influence brightness. To the extent that achromatic response mechanisms mediate brightness, chromatic annuli should affect brightness measures on the basis of luminance alone. Using flicker photometry, Kerr found very little selective effect of annuli of different wavelengths. In a brightness matching paradigm, the chromatic content of the test stimulus appeared less bright when surrounded by an annulus of similar wavelength than when surrounded by an annulus of different wavelength. Thus the same annuli that affected response in brightness matching did not affect brightness in a flicker experiment. This is evidence for an achromatic mechanism even within the chromatic channel.

DeValois and Switkes (1983) investigated masking interactions between chromatic and luminance gratings. They found that chromatic masking of chromatic gratings showed less spatial-frequency specificity than luminance masking of luminance gratings. Furthermore,

luminance gratings mask chromatic gratings of identical luminance very little, whereas chromatic gratings profoundly mask luminance gratings.

The literature on wavelength-intensity interactions in human adults, then, indicates that perception of intensity differences is greatly impaired by the presence of wavelength information.

Intensity-wavelength interactions in the pigeon. Much less attention has been given to brightness and brightness-hue interactions in the pigeon than to hue discrimination per se. Hodos and Bonbright (1972) measured threshold for detection of intensity differences with an achromatic stimulus. The procedure was a right-left successive discrimination: when a center key was illuminated with the unattenuated stimulus, a peck to the right was correct; when .8 log unit of neutral density was added a peck to the left was correct. When this discrimination was learned, the birds were tested with unattenuated stimuli versus stimuli dimmed by .4, .3 .2, .1, and .05 log unit. The mean threshold (75% correct) was .125 log unit, with a range of .05-.2 log unit.

Hodos (1969) obtained a heterochromatic brightness match from pigeons between green and yellow, red, and blue. Two birds were trained to discriminate differences in brightness between two simultaneously presented stimuli different in hue. Green light was

projected onto two keys, one attenuated by .4 log unit of neutral density. Pecks to the brighter key were rewarded; pecks to the dimmer key produced time out. When this discrimination was mastered, heterochromatic training was begun, with green versus the three other monochromatic stimuli. Initial intensity difference was one log unit; as each discrimination was mastered the intensity difference was reduced by .1 log unit until chance responding was reached. A heterochromatic brightness match was defined as a difference in intensity not noticed in two successive sessions. Results showed that birds did attend to the intensity component of the stimulus, but no other conclusions can be drawn, because no absolute intensity values were presented.

Wright (1976) obtained a hue-shift function for the pigeon, using a split key, and left-right forced choice procedure. The intensity of the comparison stimulus was raised or decreased during testing by .3 log unit. Invariant points occurred at 550 and 600 nm. At spectral extremes, there was a shift to longer wavelengths at the long end and shorter wavelengths at the short end. The magnitude of the pigeon and human hue shifts are about the same: in the central spectral region there were shifts as large as 3nm/.3 log unit. The invariant points at 550 and 600 nm correspond to points of best discrimination - as do the human

invariant points of 480 and 575 nm - suggesting common mechanisms.

Of particular interest is a control procedure described by Wright (1979) during the course of the hue discrimination experiment described earlier. Infrequent tests were made of control by intensity or wavelength by increasing or decreasing the intensity of each of the comparison stimuli. Wright reported that there was no indication of responding to intensity during these tests. This indicated that the pigeon is less sensitive to intensity than to wavelength (or that intensity is less salient when the wavelength cue is present), unlike the cat and the ground squirrels, but like old-world monkeys and other primates.

The purpose of the present study was to try to ascertain whether the oil droplets play any role in color vision. The pigeon is the species best suited for this, as so much information is available about its color vision. The unanimity of the findings of a point of best hue discrimination at 600 nm, and the imperviousness of this minimum to experimental manipulation, make a long-wavelength stimulus the obvious target of investigation. The conclusion of all theoretical models that the oil droplets serve to cut off low wavelengths and to shift spectral sensitivity

upward also suggests 600 nm as a stimulus. If the oil droplets play a role in color vision, then this role should be very detectable at 600 nm.

Normally reared birds and an expeimental bird reared on a carotenoid-free diet were taught a hue discrimination at 600 nm; the normal birds were also tested at 500 and 560 nm - a moderately good and less good area of discrimination - for comparison. Wavelength discrimination thresholds of the normal and experimental birds at 600 nm were compared to see if any significant differences in performance emerged.

A careful control for the influence of intensity cues was used, both to ensure stimulus control by wavelength and in order to further investigate hue-brightness relationships.

Although there are no reports in the literature of pigeons being reared on a carotenoid-free diet, it has been used with chicks and Japanese quail (e.g., Wallman, 1979). There are two types of precursors of vitamin A: carotenoids, which are present in vegetables, fruits, and grains, and the ester retinyl palmitate, which is obtained from animal tissue, such as fish liver. For a vegetarian like the pigeon, therefore, the only natural source of vitamin A is food containing carotenoids. It is not possible for an animal to synthesize carotemoids <u>de novo</u>; they must be present in the diet (Meyer, Stuckey, & Hudson, 1971).

Other than as a source of vitamin A, carotenoids are apparently not necessary for survival as long as synthesized vitamin A is supplied in the diet; this synthesized vitamin A should allow normal development of the visual pigments (Wallman, 1979).

Both chickens and Japanese quail are precocial, while the pigeon is altricial. If the pigeon "crop milk" (the sloughed-off lining of the epithelial layer of the crop) contains carotenoids, it is difficult to see how transmission of carotenoids to the squab could be avoided. Both chick and quail (Konishi, 1965; Cooper & Meyer, 1968) are hatched with pigmented droplets. It is not known whether the pigeon is. The extreme pallor of the squabs and the gradual darkening of their legs (Figure 1), which are colored by carotenoids, according to Levi (1974), suggest that they may not be. An attempt was made to resolve this question by examining the retina of a newly hatched squab of parents fed a normal diet.

After behavioral work was completed, the animal reared on a carotenoid-free diet was sacrificed, and its retina examined microscopically for the presence of pigmented oil droplets. A normally reared pigeon was examined for purposes of comparison.

Since vitamin A is so important to retinal functioning, some concern was felt that depriving the bird of the usual precursor of vitamin A might affect

Figure 1.

Legs of normally reared squab at ten days. Note the apparent absence of carotenoid pigment.

his cones and photopigments even though synthesized vitamin A was added to the diet. Therefore, some test of the integrity of the photosensitive elements of the retina was desirable. Microspectrophotometry or recording from single cones were thought to be techniques too risky for use with a single subject, so it was decided to perform electroretinography on the experimental bird and some normal controls.

# Method

## Subjects

Normal subjects were six white Carneau pigeons of both sexes obtained from the Palmetto Pigeon Plant in Sumter, South Carolina. They ranged in age from two to four years at the start of the study. They were maintained at about 85% of their free-feeding weight. The birds had previously been subjects in an experiment involving luminance discrimination; all birds were naive with repect to color vision testing. Two control birds were dropped after several months of training because they had not learned the discrimination.

In order to rear birds with unpigmented oil droplets, a carotenoid-free diet based on white degerminated corn meal was obtained from Genesis River Laboratories in Chagrin Falls, Ohio (see Appendix A for composition).

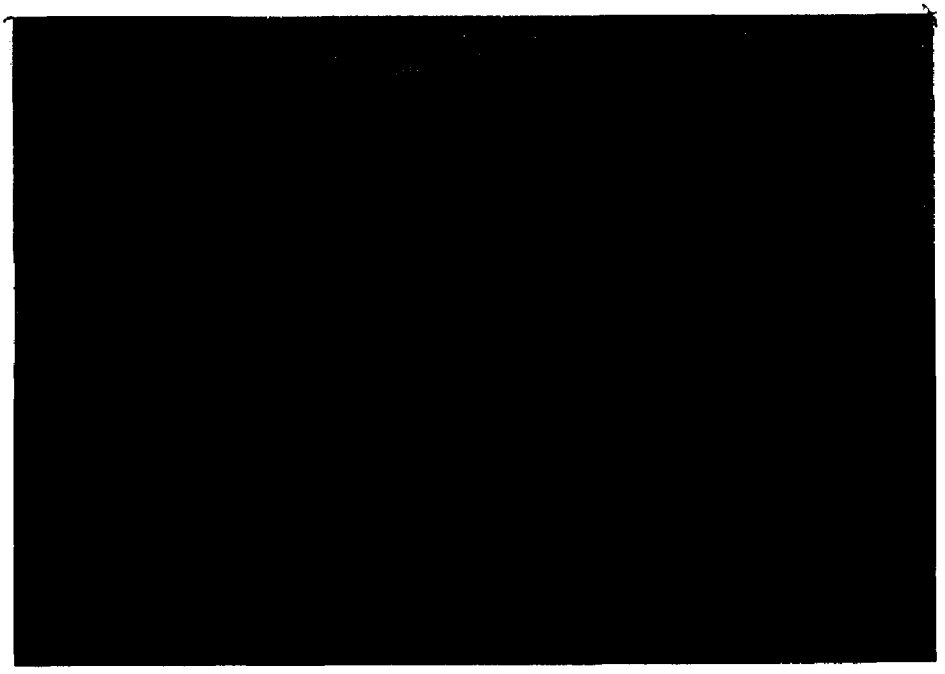
An established breeding pair of white Carneaux was obtained from the Palmetto Pigeon Plant and fed the diet for three months before being allowed to incubate their eggs. The first two clutches laid were removed and discarded, in order to deplete the yolks of carotenoids. The first clutch was hatched on January 25,1983. Both squabs appeared normal and development seemed uneventful. During the course of and after weaning, when the legs of

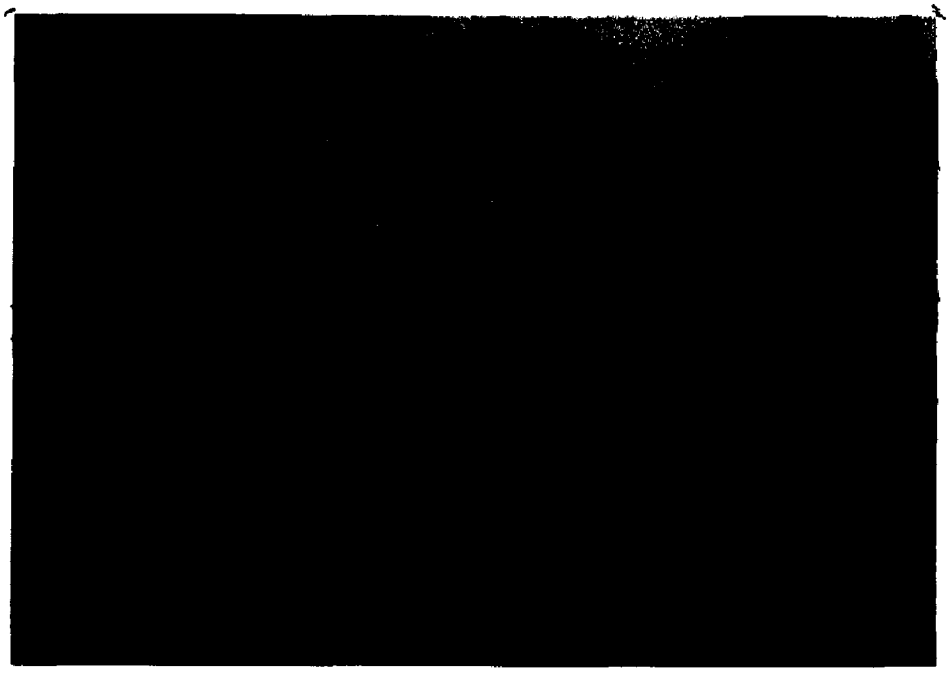
Figure 2

Carotenoid-deprived (above) and normal bird at three weeks.

Figure 3

Legs of carotenoid-deprived (above) and normal bird at adulthood.





normally reared birds begin to turn the species-typical dark red, the legs of the squabs fed the carotenoid-free diet remained the same pale pink characteristic of newly hatched birds (Figure 2). This difference persisted to adulthood (Figure 3). Otherwise they appeared perfectly normal. The first egg of a second clutch was laid on February 26, and one squab was hatched on March 16. This bird appeared to be developing normally, when it died suddenly at the age of three weeks. Autopsy indicated some abnormality in lung development, but no firm finding was made.

When the first-hatched birds were three months old, one of them began bleeding from the mouth. I took both birds to an avian veterinary, Dr. Eileen Rowan of Franklin Square, New York. Decision was made to euthanize the hemorrhaging bird, but it died befre a drug overdose could be administered. Tissues were sent for histological examination to the Department of Avian and Aquatic Medicine of Cornell University. The findings were as follows: death was due to the aspiration of blood, whose origin was unknown. The liver showed mild hydropic change of hepatocytes in portal regions. The spleen showed occasional microfoci of lymphoid cell necrosis in germinal centers. The kidney, crop, heart, larynx, skeletal muscle and small intestine were normal.

Blood specimens were sent to Dr. Josh Dein at the Washington (DC) Zoo. He reported that red blood cells were

greatly enlarged; were, in fact, two times larger than the normally larger white blood cells. He was unable to determine the cause of this abnormality.

The other bird of this clutch was found to have a heart murmur and bradycardia. The source of the murmur was not known; the electrocardiogram was normal.

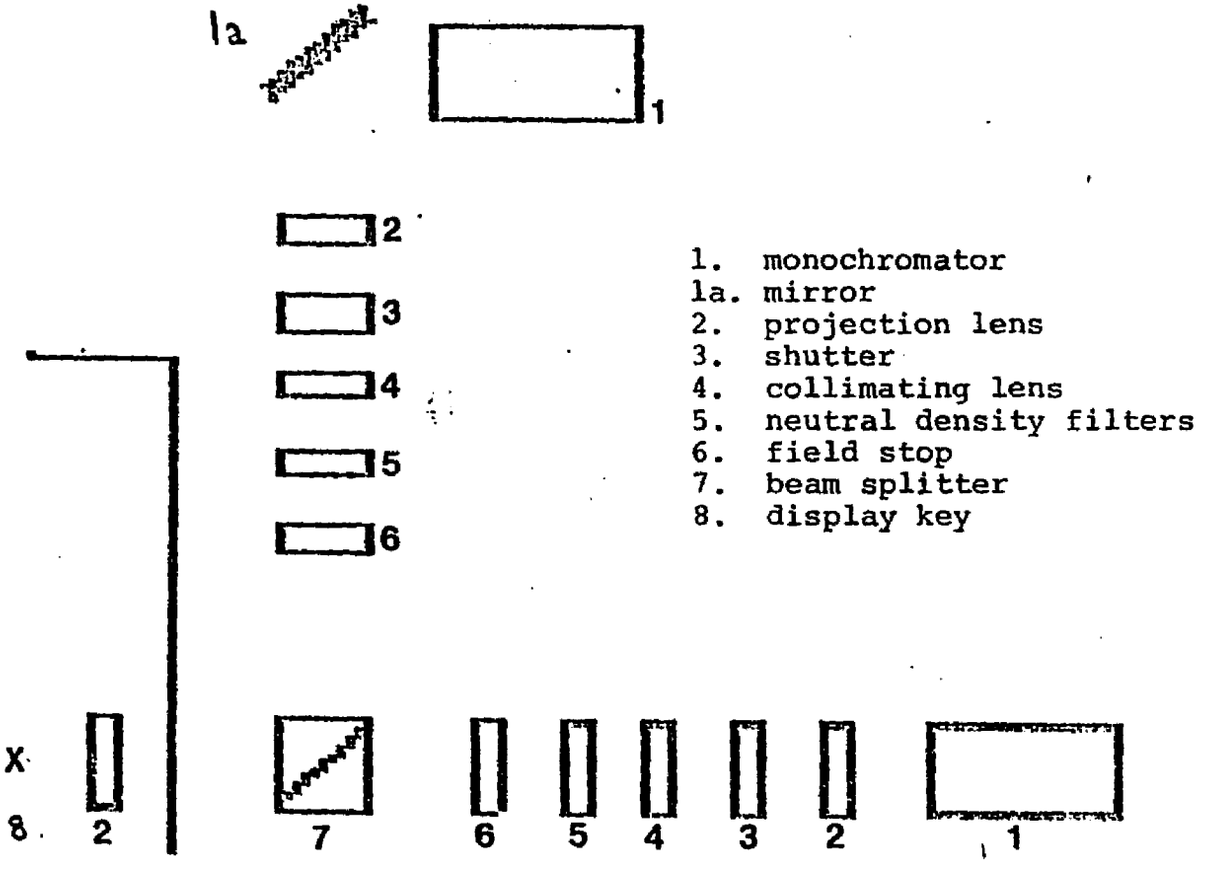
A decision was made not to rear any more squabs on the carotenoid-free diet. Although it was not specifically implicated in the deaths and abnormalities, it seemed likely that it was in some way involved, an inference strengthened by the fact that the parents subsequently reared two birds who attained normal adulthood after the parents were returned to a grain diet. The surviving bird was maintained on the carotenoid-free diet, without our having any real hope of being able to test his color vision. When this bird was about one year old, he still appeared to be perfectly fit, indeed he seemed exceptionally robust, and the decision was made to begin training.

## Apparatus

A two-channel optical system was used (diagrammed in Figure 4). In Channel A a Bausch and Lomb monochromator (Cat# 33-86-76) provided a variable stimulus, using a 45-watt tungsten halogen T2.5Q bulb operated at 6 amp. The beam was passed through a focussing lens, a shutter, a

Figure 4.

Schematic diagram of optical system.




1. monochromator
1a. mirror
2. projection lens
3. shutter
4. collimating lens
5. neutral density filters
6. field stop
7. beam splitter
8. display key

collimating lens, a circular neutral density wedge, a field stop,a beam splitter, and a projection lens. In Channel B the standard stimulus was generated by a monochromator identical to the one in Channel A. The beam was passed through a focussing lens, a shutter, a collimating lens, neutral density filters as needed, a field stop, a beam splitter, and a projection lens. Both channels converged on the center key of a three-key intelligence panel placed in a standard pigeon chamber, forming a bipartite field.

The chamber (BRS/LVE SEC-002) was 62.2 cm high, 35 cm wide, and 30 cm deep. A fan in the chamber provided ventilation, and masked noise from outside the box. The two side response keys were 2.5 cm in diameter; the diameter of the bipartite field of the monochromatic light stimulus presented on the center key was 4 mm. All three keys were covered with Lenscreen (Edmund Scientific) so that light stimuli were diffused evenly over the keys. The two side keys were illuminated by 28-volt (#1819) lamps. The distance between each key was 5.7 cm; the top of the magazine was 10.3 cm above the floor of the box. The magazine light was a Sylvania 48 ESB bulb. The houselight was a Chicago Miniature 1820 bulb, recessed in a hole in the ceiling of the chamber.

Presentation of stimuli in the chamber and recording of responses were controlled by a Radio Shack Model III computer with an Interfacer 80 (Alpha Products, Queens, New York). The interfacer was also connected to a shutter

driver (Uniblitz Model 325B, Vincent Associates, Rochester, New York), which opened a shutter in each channel to form the bipartite field display on the center key of the intelligence panel (BRS/LVE PIP-013). The interfacer also ran two stepping motors (Airpax Series 82800). One controlled the wavelength of the stimulus provided by the monochromator, the other moved a circular variable density wedge to control the intensity of the stimulus.

Three stimuli were used as standards: 500, 560, and 600 nm. Intensity for each stimulus was adjusted for pigeon luminosity by adjusting relative intensity between stimuli based on the physical energy emitted at each wavelength (as measured by a UDT Model 40A photometer) and then by using Blough's (1957) photopic luminosity curve for the pigeon (see Appendix B for actual radiances of stimuli used).

## Procedure

A two-key forced-choice procedure was used. Normal birds were first hand-shaped to peck a display key transilluminated by white light, then they were trained to peck sequentially the display key and one of two (alternating randomly) illuminated response keys. In the next training procedure the split key was introduced: one half of the key was lit with monochromatic (600-nm)light that served as a standard stimulus throughout the session, the other half was lit with a monochromatic stimulus whose

wavelength was varied among 590, 600, and 610 nm. Presentation of the stimuli varied randomly, with the restriction that each stimulus be presented the same number of times. Thus at 600 nm, a bird was presented with a split key of which both sides displayed a light of 600 nm, or one half showed 600 nm and the other 590 or 610 nnm. Only one variable stimulus was used for each bird; two birds were first trained to discriminate between 600 and 610 nm and two to discrimnate between 600 and 590 nm; when each bird had learned its first discrimination, it was then trained on the other. (All birds were first trained with the 600-nm standard stimulus, despite the possible effects of order of learning on later performance, because it is wavelength discrimination in this 600-nm region of the spectrum that is the main focus of this study.) If the variable stimulus was the same as the standard, a peck to the display key and then the right response key was correct; if it differed, a peck to the display key and then the left response key was correct. In this training procedure no errors were permitted: after the display key was pecked, only the correct response key was lit and a response to this key was rewarded with 4-sec access to grain. A peck to the unlit response key had no consequences. Each training session consisted of 80 trials, and the procedure was continued for ten sessions. during training, continuous reinforcement was used. Throughout the study dove mixture was used as a reinforcer,

since the grains are smaller than those of pigeon mix and thus more reinforcement could be given without affecting the birds' weight. For the carotenoid-deprived bird the diet pellets were used as reinforcement rather than grain. Since the pellets could not be cut into pieces as small as the dove mix, in order to maintain his deprivation weight this bird was run on the average only three out of five days rather than five out of five, as the normal birds were.

In the next training procedure errors were permitted. The same stimuli were presented, but when the display key was pecked both response keys were lit. A peck to the correct key was rewarded with 4-sec access to grain; an incorrect response produced a 10-sec time out, and turned off the houselight. A correction procedure was used in case of error: after the time out the display key was lit with the same stimulus that had been incorrectly identified. The houselight was also lit. Following a peck to thedisplay key, both response keys were lit, and a peck to the correct side key produced a 2-sec access to grain. A further incorrect response had the same consequences; retrials continued until the correct response was made.

The houselight was used during the 10-nm discrimination training at 500 nm, because it was felt that darkening the houselight would be a useful indicator to the bird that it had made an error. When the first discrimination was learned, however, the houselight was disconnected and the

only illumination came from the display key, the response keys, and magazine light.

In order to rule out the possibility that discrimination was based on luminance rather than wavelength, a procedure was instituted by which the comparison stimulus could vary by .1 log unit of intensity on either side of the standard. That is, the comparison stimulus could be .1 log unit more intense than, equal to, or .1 log unit less intense than the standard stimulus. The .1-log unit interval was chosen to avoid contamination by the Bezold-Brücke effect (the change in appearance of hue with intensity change), which might occur if larger intensity increments were used. The .1-log unit interval should be adequate as a brightness control, because only small wavelength differences were used, differences which produce very small changes in luminosity (see Appendix B for actual values). And, as DeValois, et al. (1974) pointed out, adequacy of the brightness control can be assessed from the discrimination performance: if the birds were using the intensity cue, performance should not deteriorate as the wavelength interval decreases, as long as the intensity difference remained. Conversely, if the birds paid no attention to intensity, no pattern of responding to the intensity of the stimulus should be evident. The presentation of the three intensity levels was varied randomly. The "correct" response was based on wavelength alone. That is, if a bird responded "same" when intensity was adjusted for equal

pigeon luminosity and wavelength was different, the response was considered incorrect.

When criterion responding (90% correct or better for three successive days) was reached at 10 nm, a new discrimination was begun. The variable stimulus was made 1 nm closer to the standard, and sessions continued until criterion was reached. At stimulus differences too small for criterion to be attained, training continued until responding appeared to the experimenter to become stable; data were used for the final three days.

Two other standard stimuli were used in addition to 600 nm: 500 and 560 nm. For these stimuli it was necessary to increase the initial wavelength difference to 20, or in some cases, even 30 nm, in order to attain criterion responding, because of a decreased sensitivity to wavelength differences at these wavelengths compared to 600 nm.

The carotenoid-deprived bird was taught only the wavelength discrimination at 600 nm.

When all wavelength discriminations were completed, a series of intensity-only discriminations was taught. The two halves of the display key both showed the same wavelength, but intensity was varied. This intensity-only discrimination was attempted at all three standard wavelengths. Intensity training was begun with the variable stimulus at .3 log unit more or less intense than the standard, and, when criterion was reached, decreased by

.05 log unit until chance responding (50% correct) was reached.

The actual number of trials for a bird in any session varied: the computer was programmed to end a session after any consecutive 80 trials during which fewer than 10% errors were made. Thus a bird could run as few as 80 or as many as 250 trials. When a bird was no longer able to reach criterion the session ended at the expeimenter's discretion - usually at about 150 trials. Data analysis was based on the final 80 trials of a session.

After the first discrimination had been learned, grain reinforcement was reduced to a random ratio schedule of 20%; the other trials were reinforced by magazine light alone. Grain (or pellet) reinforcement on correction trials was discontinued for four of the five birds. For one bird, who learned extremely quickly, primary reinforcement was continued on correction trials, lest learning be disrupted.

## Electroretinography

The birds were injected with ketamine (100 mg/ml) intraperitoneally, at a dose of 3 ml/kg body weight. This very high dose of ketamine must be given IP, as it is fatal if given intramuscularly. It produces a good preparation for ERG testing, as the bird is quiescent for at least two hours, and the eyes remain open. Recovery is prolonged but

uneventful; all injected birds survived.

The cornea of the recording eye was anesthetized by one or two drops of proparacaine (.5%) prior to the insertion of a contact lens bearing a small chlorided silver electrode. The reference point was a Grass gold disc electrode placed on the scalp, held in place with Grass electrode paste. The nictitating membrane was not excised. A high-gain, low-noise preamplifier (Rockefeller University electronics shop) with high-frequency cutoff set at 530 Hz and low-frequency cutoff set at 1.6 Hz was used to amplify the signal.

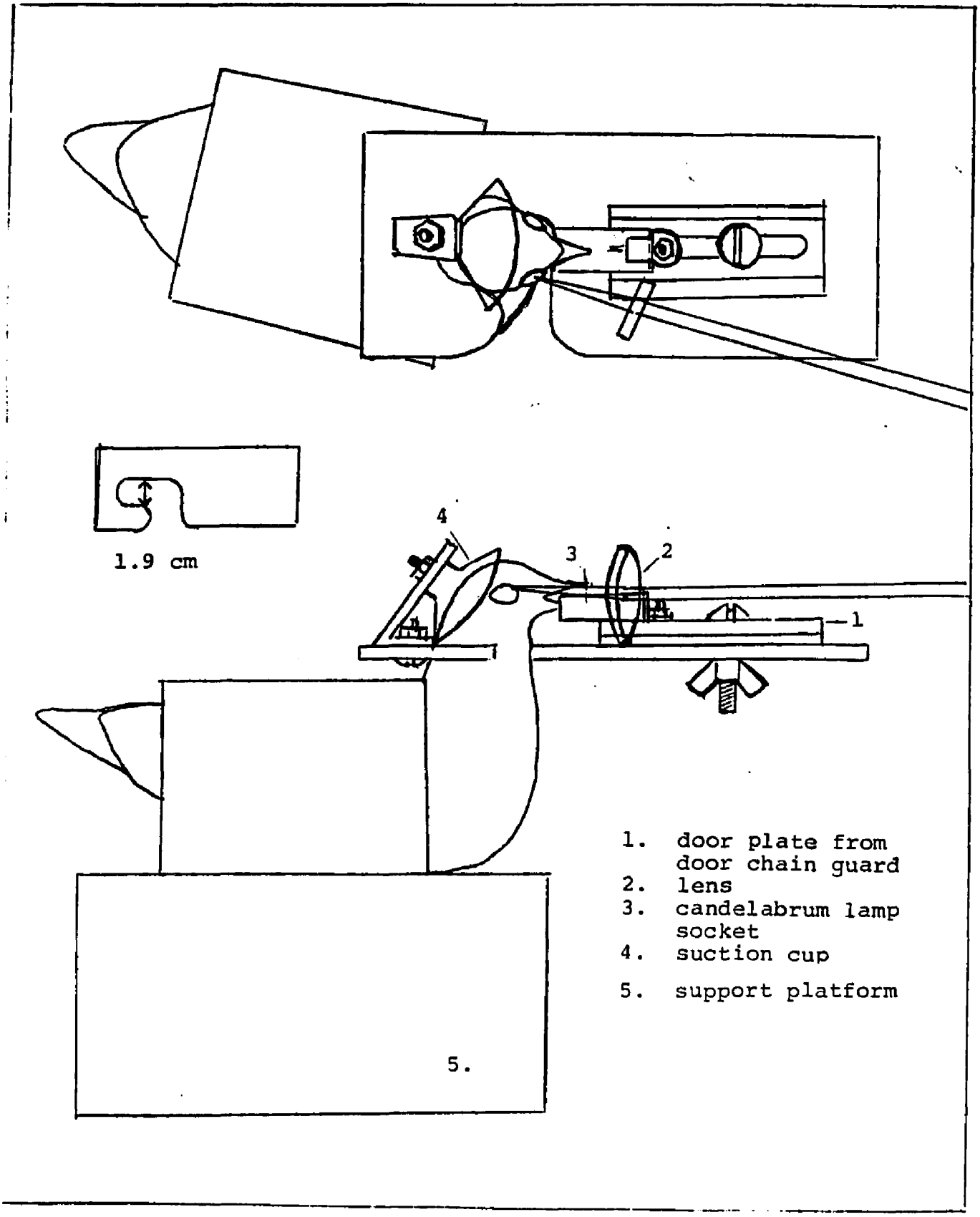
During testing the birds were restrained in the apparatus shown in Figure 5. The lower mandible was placed in a small socket filled with modeling clay. The neck was supported in a lucite holder, and the head braced by a plastic suction cup. The body was wrapped in a plastic sleeve and supported on a platform.

The light stimulus was presented through one channel of the optical system described earlier; the fixation of the head allowed the stimulus to be presented in Maxwellian view. The stimulus subtended a visual angle of 21°. The bird was positioned so that the light beam entered the eye frontally, in order to stimulate the red field (temporal retina). The beam of light was flickered at a rate of 16 Hz, to minimize rod responses.

Wavelengths from 540 (520 for the carotenoid deprived bird) to 660 nm were used, at 20-nm intervals. Four

Figure 5.

Apparatus used to restrain the birds during electroretinography.




1. door plate from door chain guard
2. lens
3. candelabrum lamp socket
4. suction cup
5. support platform

intensity levels were used: 0, .3, .6, and .9 log unit of attenuation from the maximum available at each wavelength (Appendix B).

The amplified electrical response from the eye was sampled every 4 msec by a V-2 visual stimulator (Rockefeller University electronics shop; described in Milkman, Shapley & Schick (1978), digitized with an 8-bit A/D converter and signal averaged. For each stimulus presentation 128 responses were averaged, which at a 16 Hz flicker rate, yielded a stimulus duration of 8 sec. A Tektronix (Portland, Oregon) 5115 storage oscilloscope was used to monitor the ERG responses and a Tektronix Type 502A oscilloscope monitored averaged responses. Averaged responses were printed out on a Brush 2400 recorder (Gould Instrument Co., Cleveland).

Two sessions were run with each of two normal birds, and two with the carotenoid-deprived bird.

## Histology

The retinas of the carotenoid-deprived bird, that of a normally reared adult pigeon, and a squab at 18 days of incubation were examined for the presence of visibly pigmented oil droplets. For examination of the squab retina, a pigeon was removed from the egg while it was pipping. The bird was dark adapted for an hour, and then

overdosed with with 1 cc morphine, IM. The adult birds were dark adapted for one hour, and overdosed with 3 cc of nembutal, IM. For examination of the oil droplets, each eye was excised, dissected around the ora serrata, and the retina teased out in saline. The pigment epithelium was detached from the retina. Each retina was mounted receptor side up on a slide and covered with a cover slip. The retinas were examined under an Olympus (Model BH-2) microscope (at 40x and 400x) and photographed with an Olympus camera. Film used was Kodachrome 64, with 78a filter.

In a further attempt to confirm that the retina was normal except for the oil droplets, anatomical light microscopy investigations were performed by Dr. Katherine V. Fite of the University of Massachusetts at Amherst. Sections from the red field, foveal area, and yellow field of the retinas of the carotenoid-deprived and a normal bird were examined.

The eyes were removed after the birds had been injected with the lethal dose of nembutal and showed no corneal reflex. The eyes were cut around the anterior chamber and submerged in a fixative of 1.25% glutaraldehyde and .90% paraformaldehyde in a .12M phosphate buffer with .02% $CaCl_2$. for two hours. After that time the anterior chamber was removed and the vitreous extracted. The eye was stored in 70% alcohol.

# Results

## Wavelength discrimination

Prior studies were unanimous in their finding that pigeons' wavelength discrimination is excellent at around 600 nm. Agreement was not so complete concerning discrimination at other areas of the spectrum. Wright (1972), for example, found minima at 500 and 540 nm, as well as at 600 nm, whereas P. Blough (1972) found a sharp decrease in discrimination ability at 500 nm. Results of the present study were similar to earlier findings in that performance was best at 600 nm.

The discrimination curves for the normal birds at 600 nm are shown in Figure 6. It is obvious that discrimination is excellent. Criterion responding (90% correct) is maintained until the distance between standard and comparison stimuli is 4 or 5 nm, on both sides of 600 nm. Difference threshold (the wavelength interval at which performance is 75% correct) is on the average 2.8 nm, on both sides of 600 nm. Even at a 1-nm difference, responding has not fallen to chance for most birds. The other striking fact about the birds' performance is how similar to each other the curves are; there was very little intersubject variability.

Figure 6.

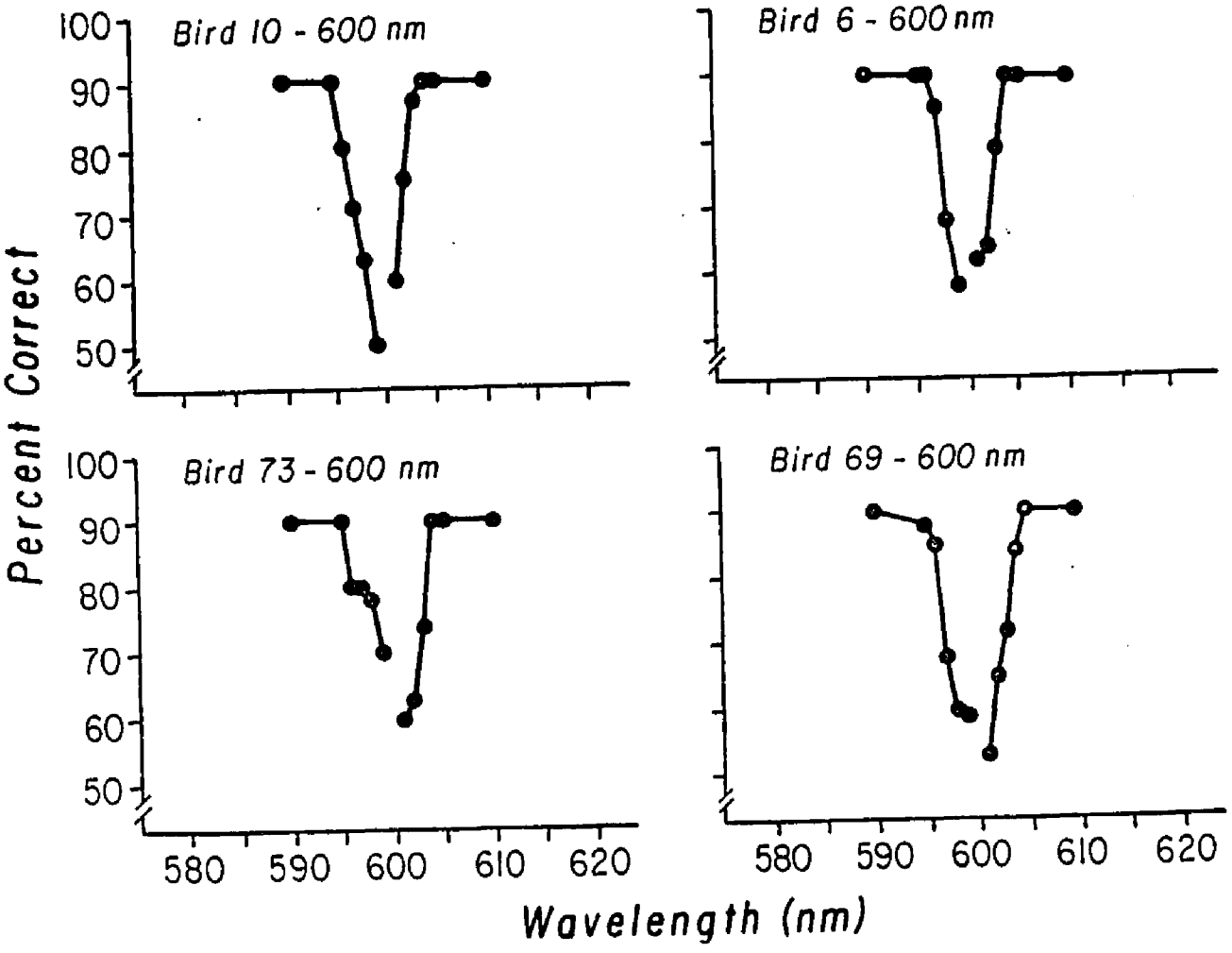
Wavelength discrimination performance for the four normal birds when the standard stimulus was 600 nm. Sensitivity is scaled in terms of percent correct. On the horizontal axis is wavelength difference of standard and comparison stimuli, in nanometers. Each data point represents a discrimination between the standard stimulus and the wavelength at the data point.

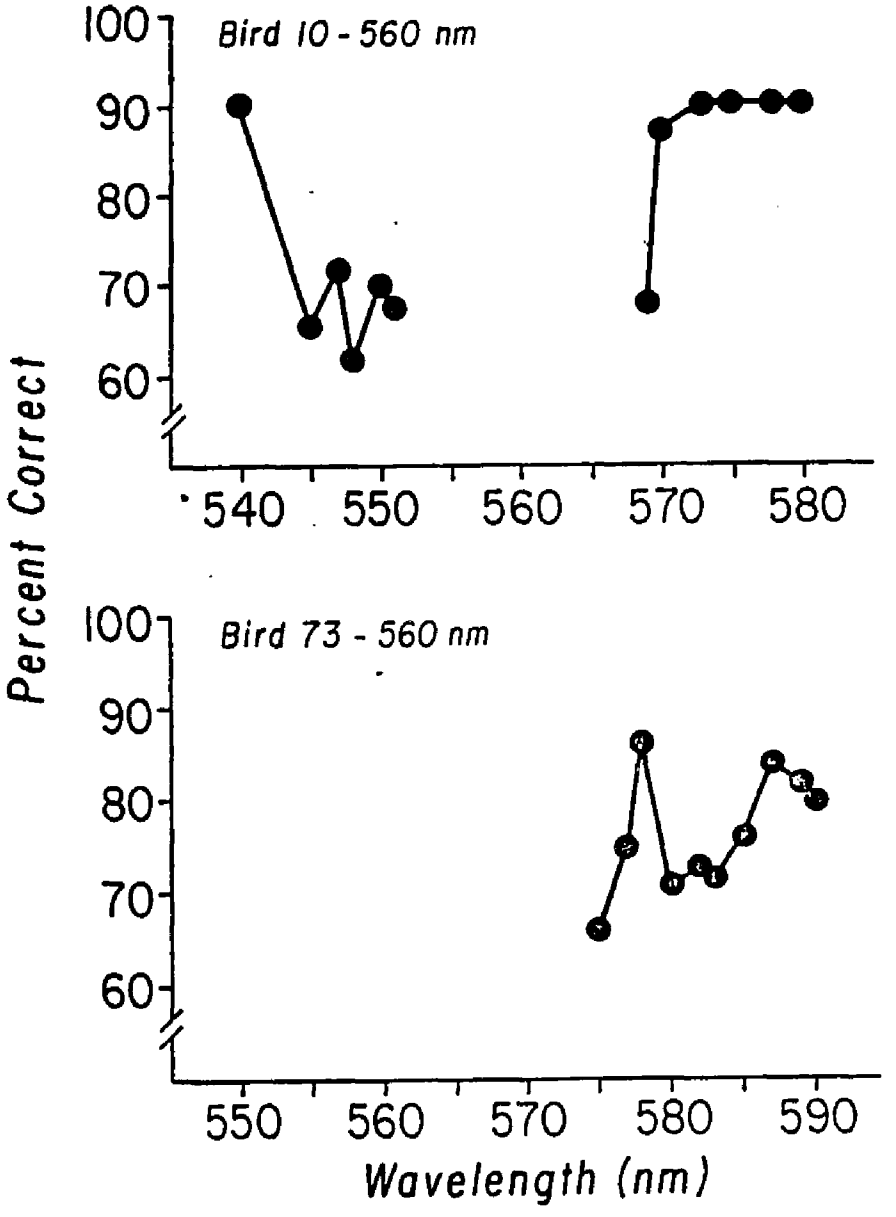
Figure 7.

Wavelength discrimination performance for Birds 10 and 73 when the standard stimulus was 560 nm. Axes as in Figure 6.

Figure 8.

Wavelength discrimination performance for Birds 6 and 69 when the standard stimulus was 500 nm. Axes as in Figure 6.


Bird 10 - 600 nm
Bird 6 - 600 nm
Bird 73 - 600 nm
Bird 69 - 600 nm
Percent Correct
100
90
80
70
60
50
580
590
600
610
620
Wavelength (nm)


Bird 10 - 560 nm
Bird 73 - 560 nm
Percent Correct
100
90
80
70
60
540
550
560
570
580
590
Wavelength (nm)

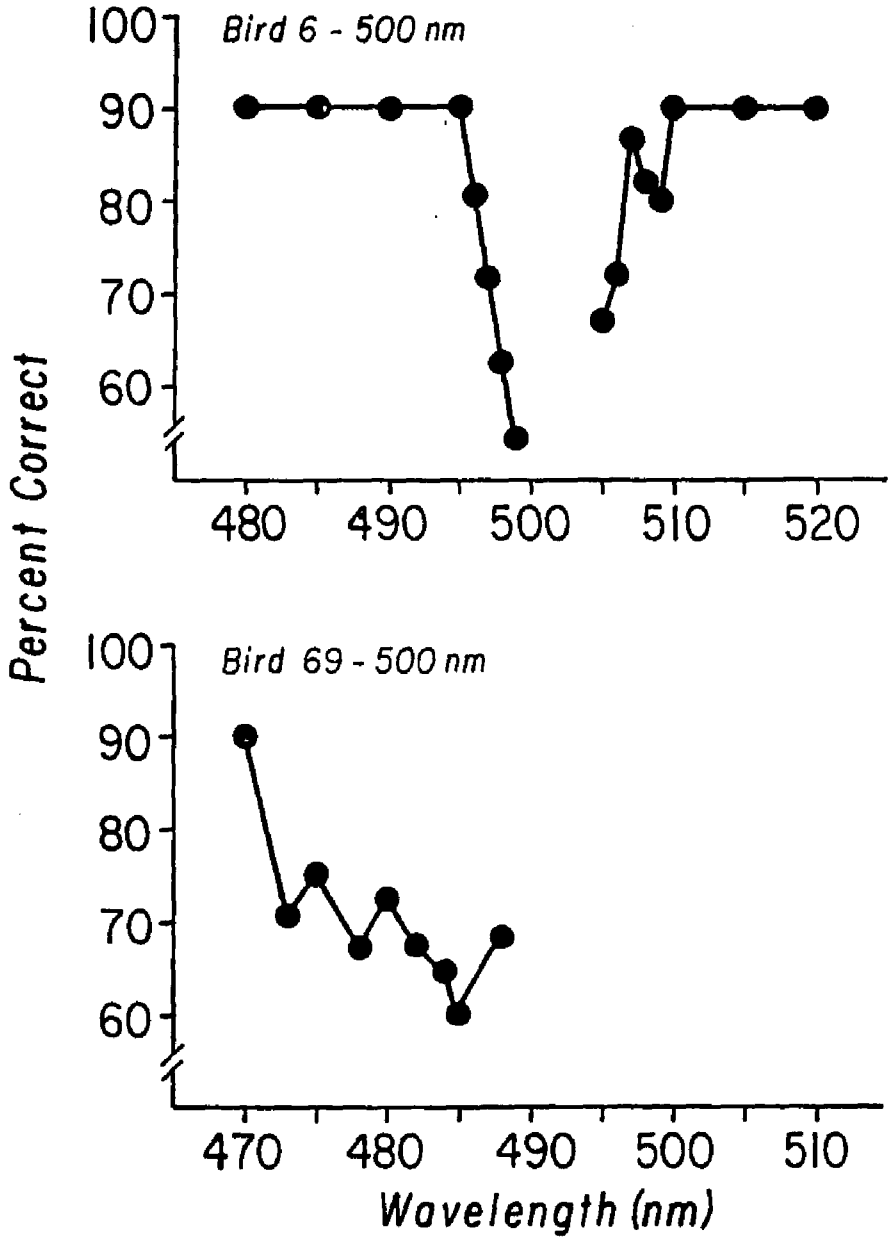

Bird 6 - 500 nm
100
90
80
70
60
480
490
500
510
520
Bird 69 - 500 nm
100
90
80
70
60
470
480
490
500
510
Percent Correct
Wavelength (nm)

Figure 7 shows the performance of two birds at 560 nm. Note the increase in the initial discrimination interval to 20, or in the case of Bird 73, to 30 nm. Even in the one case (Bird 10 at 560/580 nm) where the curve resembles the curves at 600 nm, criterion responding is maintained only until the stimulus interval is 13 nm; threshold (75%) responding occurs at between 9 and 10 nm, and responding has fallen to 68% at 9 nm. In the other curves shown, performance is both much poorer and much more variable than at 600 nm. For Bird 10 at 560/540 nm, criterion responding occurs only at 20 nm; threshold is at 14 nm. For Bird 73, criterion could only be reached when the stimulus interval was 30 nm. Figure 8 shows the performance of two birds at 500 nm. Bird 6 did about as well as at 600 nm when comparing 500 and 480 nm; criterion responding was maintained until a 5-nm difference was reached. Difference threshold was at 3.5 nm, and chance responding occurred only at 1 nm. She did not do quite so well at the other side of 500 nm: criterion responding was maintained only up to a 10-nm difference; 75% correct occurred at a 6.5-nm difference. Training ceased at a 5-nm interval, because the bird began to behave in an agitated manner prior to being put in the experimental chamber. Bird 69 was very poor at this discrimination. It took many months of training before criterion was reached at a 30-nm interval; criterion was not reached at smaller intervals. Difference threshold was reached at 25 nm. The 500/520 comparison was

not attempted with Bird 69.

In Figure 9 is shown a comparison between the mean performance of the normal birds at 600 nm (upper half of the figure) and the performance of the carotenoid-deprived bird (Bird 99). There is an obvious and dramatic decrement in the ability of the deprived bird to discriminate. On the long wavelength side of 600 nm, he showed no movement away from chance responding, even for a 20-nm difference between standard and variable stimuli. At the other side of 600 nm he could discriminate 570 from 600 nm, but criterion responding was maintained only up to a 23-nm stimulus difference; difference threshold was at 21 nm, and responding had fallen to chance levels by 18 nm. This bird was not tested at other spectral regions.

Figure 10 shows length of time in 5-session blocks until criterion was reached for the initial discrimination at 600 nm. In the upper half of the figure is shown length of learning time for the four normal birds and the carotenoid-deprived bird at 600 nm versus shorter wavelengths. The range of learning time is 33 days to 40 days, with a mean learning time of 37.2 days for all five birds. Thus although the stimulus interval had to be increased to 30 nm for Bird 99 to learn the discrimination, his acquisition time was similar to that of the normal birds.

Learning time for the five birds at 600 nm vs longer wavelengths is shown in the bottom of Figure 10. Bird 99

Figure 9.

Comparison of mean performance of normal birds with carotenoid-deprived bird when the standard stimulus was 600 nm.

Sensitivity is scaled in terms of percent correct. The horizontal axis shows the distance in nanometers between the standard stimulus and the comparison stimulus. Each data point represents a discrimination between the standard and the wavelength shown at the data point.

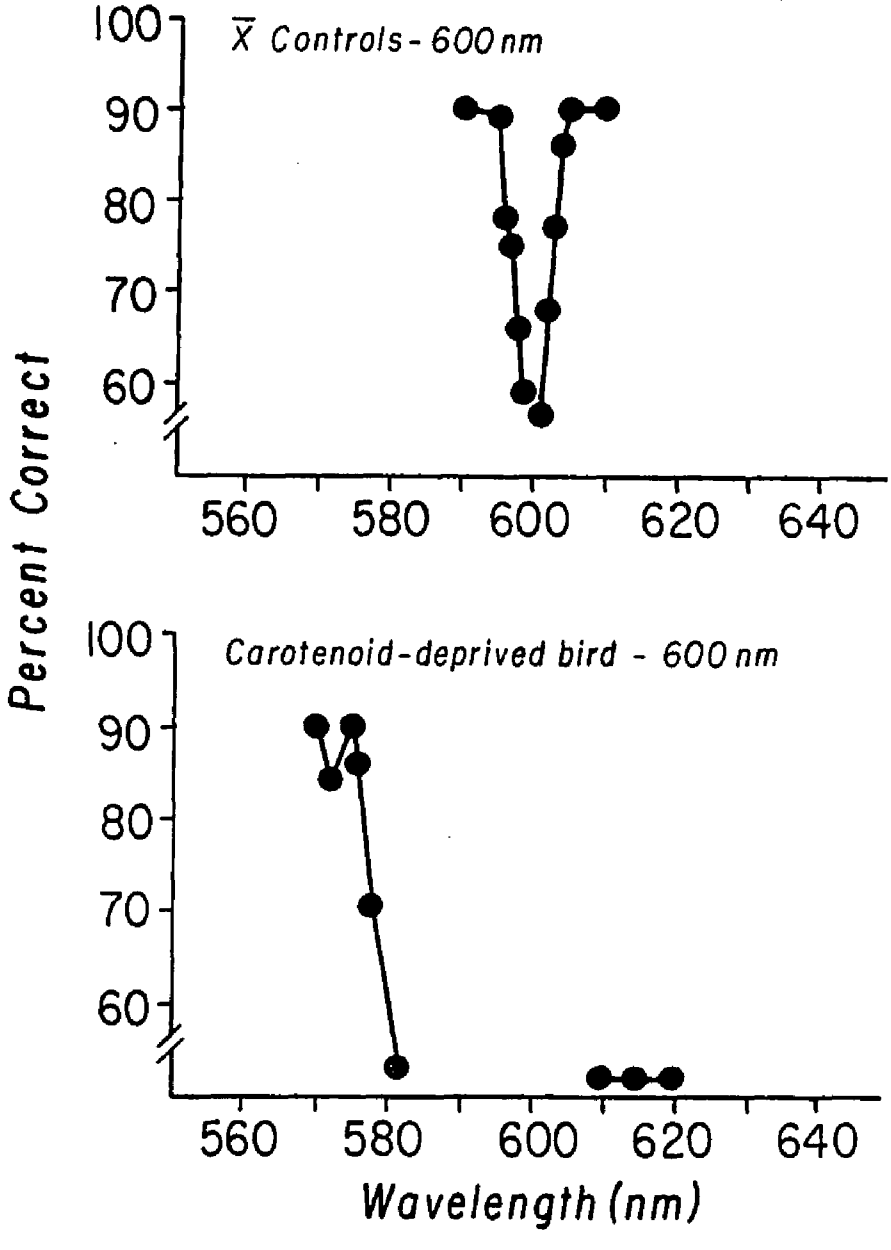
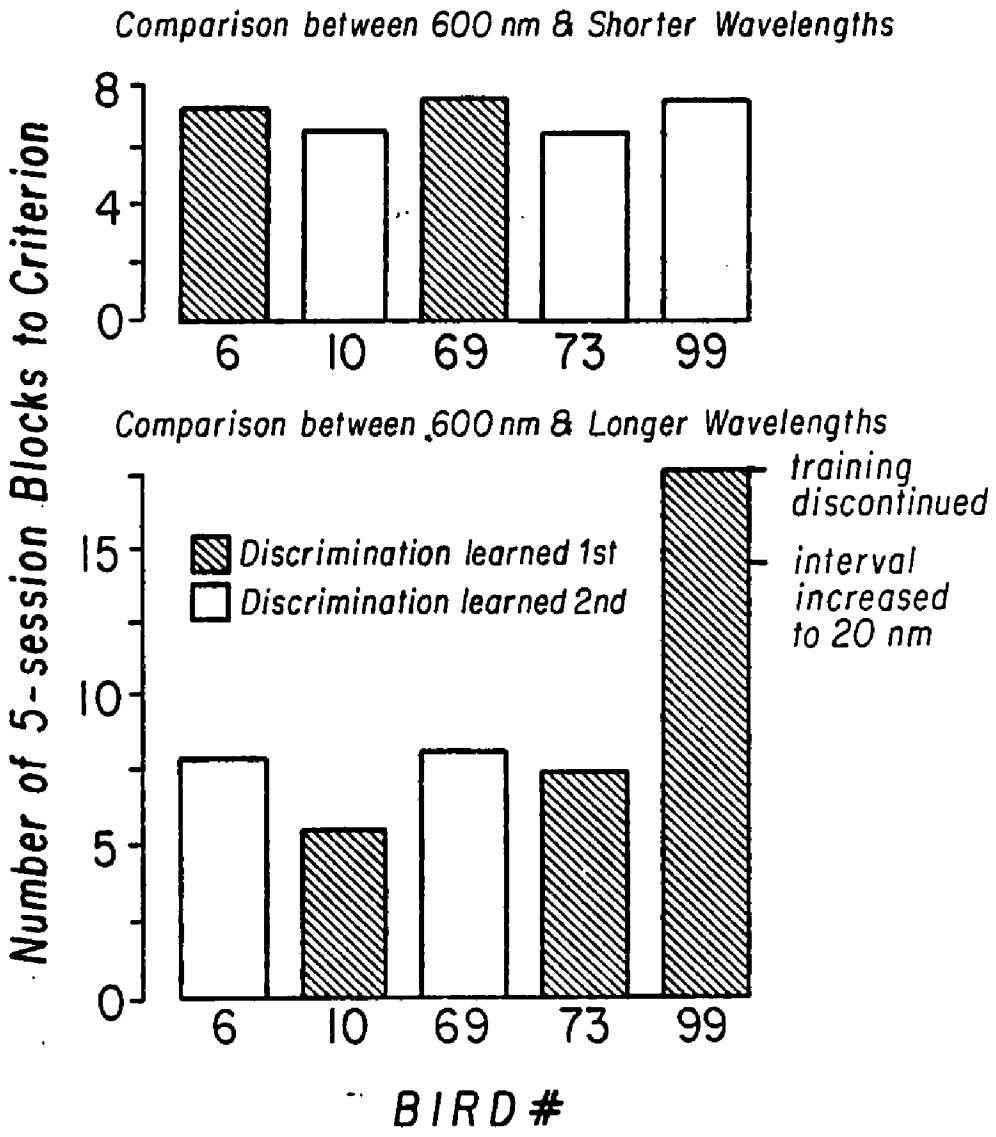

X̄ Controls - 600 nm
Carotenoid-deprived bird - 600 nm
Percent Correct
100
90
80
70
60
560
580
600
620
640
Wavelength (nm)

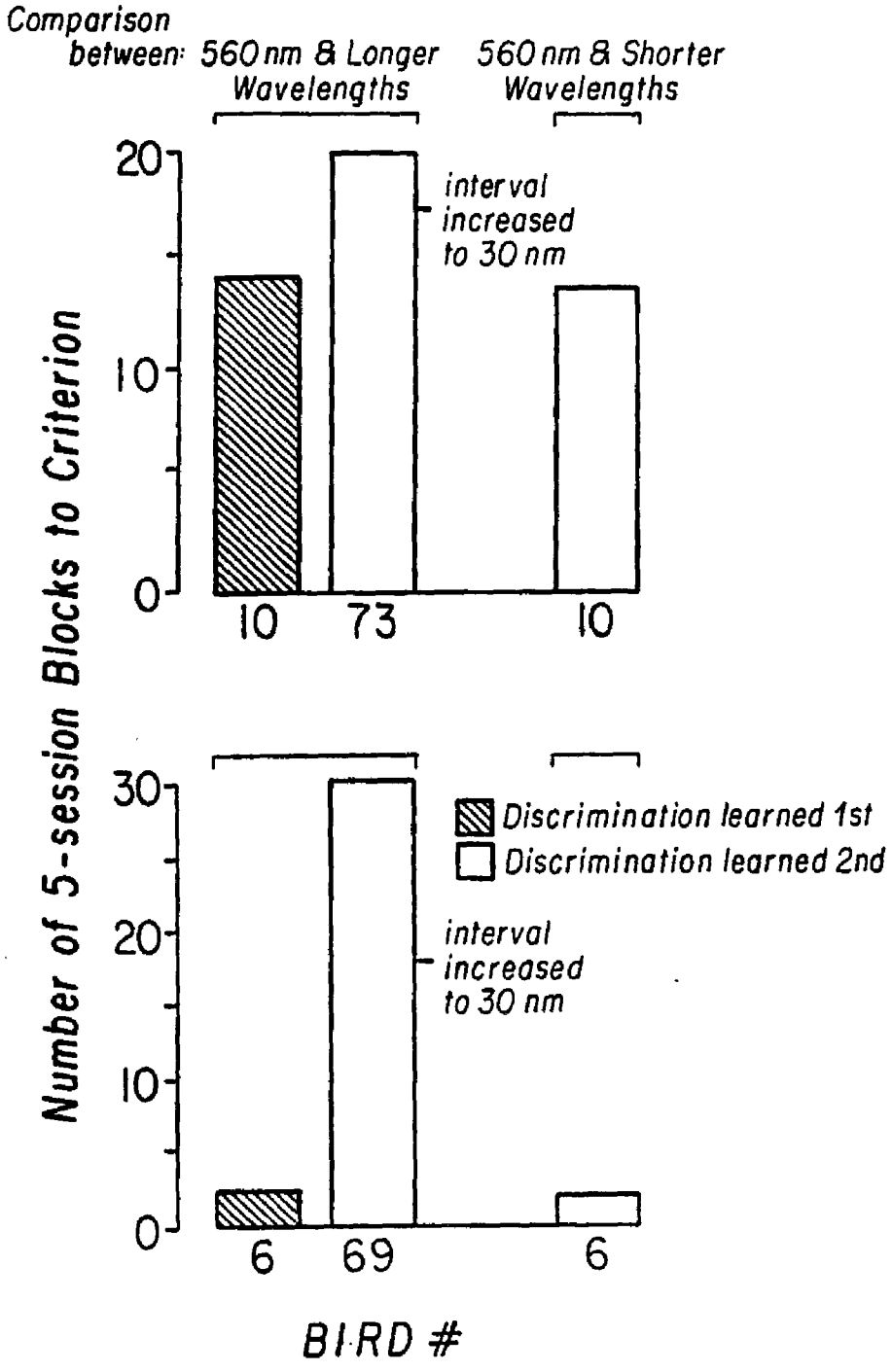
Figure 10.

Learning time to criterion for the four normal birds and the carotenoid-deprived bird when the standard stimulus was 600 nm. On the vertical axis is number of 5-session blocks until criterion was reached for the largest wavelength interval learned. The shaded box represents the first-learned discrimination for each bird.

Figure 11.

Learning time to criterion for the four normal birds when the standard stimulus was 500 (above) or 560 nm. Axes as for Figure 10.


Comparison between 600 nm & Shorter Wavelengths
8
4
0
6
10
69
73
99
Comparison between 600 nm & Longer Wavelengths
training discontinued
interval increased to 20 nm
Discrimination learned 1st
Discrimination learned 2nd
15
10
5
0
Number of 5-session Blocks to Criterion
6
10
69
73
99
BIRD #


Comparison between:
560 nm & Longer Wavelengths
560 nm & Shorter Wavelengths
20
10
0
interval increased to 30 nm
10
73
10
30
20
10
0
interval increased to 30 nm
6
69
6
Discrimination learned 1st
Discrimination learned 2nd
Number of 5-session Blocks to Criterion
BIRD #

never learned this discrimination. For the other birds, range of learning time was 30 to 43 days, with a mean of 39 days.

Figure 11 shows learning times for the other discriminations. The upper half of the figure shows learning time for Birds 10 and 73 at 560 nm; the lower half shows Birds 6 and 69 at 500 nm. Note the increase in intersubject (though not intrasubject) variability at these wavelengths. Bird 10 learned 560/580 nm in 70 days and 560/540 nm in 68 days. Bird 73 required 105 days to reach criterion at 560/590 nm. Bird 6 learned both 500/480 nm and 500/520 nm very rapidly, in 13 and 10 days, respectively. Bird 69 finally reached criterion responding at 500/470 nm after 150 days. It should be borne in mind that these learning times represent only the length of time required to reach criterion at the largest wavelength interval. Data were collected at smaller intervals, usually until chance responding was reached, so that, for example, the total number of days spent testing Bird 69 at 500 vs shorter wavelengths was 253. This is why Birds 69 and 73 were not tested at both sides of their respective standard stimuli.

Another question that might arise is why training of the carotenoid-deprived bird (Bird 99) was abandoned after 94 days, when it took Bird 69 150 days to reach criterion. The reason, not apparent in a bar graph, is that Bird 69's performance showed a consistent (if very gradual)

improvement, while Bird 99's performance over 94 days stayed essentially at chance levels.

## Effect of intensity

The next group of figures shows in what way the birds responded to the intensity component of the color stimulus. Sensitivity is scaled in terms of d' for the following reasons. These figures consider responding on only one key, the "different" key, and if percent correct were used as a sensitivity measure there would be no way to assess overall performance: perfect responding could mean either that the bird was discriminating perfectly between the standard and comparison stimuli or that response bias was causing a bird to peck only the "different" key. The use of d' allows performance on both keys to be assessed without response bias. The value of d' was derived in the following way: correct recognitions of the "different" stimulus were judged to be hits, while incorrect identification of the "same" stimulus as "different" was counted as a false alarm. Scores for three days were averaged, and the d' value was read from the d' table in Swets (1964). The curves each show the data for one wavelength interval between standard and comparison stimuli; the curve labeled "10," for instance, means that the standard and comparison stimuli were separated by a 10-nm interval.

If the birds were responding solely or mainly on the

basis of stimulus intensity, then performance should not deteriorate as the wavelength difference became smaller, since the intensity interval remained the same. In this case, one might expect to see a family of V-shaped functions, with better performance at higher and lower intensities and poor performance at equal intensity.

On the other hand, if the birds were completely insensitive to stimulus intensity, the curves should show no recurrent pattern of responding that might indicate that performance was enhanced by having intensity information.

Figures 12 through 14 show responding of the normal birds at 600 nm, with three intensity differences: .1 log unit less than, equal to, and .1 log unit greater than the standard stimulus. Note that the birds seem completely indifferent to intensity information until the wavelength intervals are very small: the curves show no consistent V-shaped pattern of responding at large intervals. Birds 6 and 10 apparently begin to use intensity information only at 2 and 1 nm, respectively; that is, only when there is virtually no wavelength information available. Birds 73 and 69 do not show this pattern strongly. The intensity difference was then increased to .2 log unit for these birds for the last few intervals of their second discrimination, as shown in Figure 14. The steep V-shaped curves similar to those of Birds 6 and 10 then do appear at the 1-nm interval.

The method of planned comparisons (Hays, 1963) was used

to assess whether the apparent differences in performance at 1 or 2 nm compared to larger intervals were significant. Performance at a one-nm or one and two-nm interval was compared with performance at larger wavelength intervals by weighting the one- (or one and two-) nm curve, and counterweighting the other curves appropriately. T tests were performed on the scores derived in this way. Significant t's were obtained for the following discriminations: Bird 10 at 600/610 nm ($t(13)=2.07$; $p<.05$), Bird 69 at 600/610 nm and a .2-log-unit intensity difference ($t(7)=2.24$; $p<.05$), and Bird 73 at 600/590 nm and a .2-log-unit intensity difference ($t(7)=1.93$; $p<.05$). for Bird 6, t's of 1.32 at 600/610 nm and 1.36 at 600/590 nm approached significance ($t(13)<.10$) (values of t are shown on each graph). Thus three of the four birds showed a significant effect of responding to intensity only in the virtual absence of wavelength information at 600 nm.

The data for the bird on the experimental diet are plotted in Figures 15 and 16. At 600/620 nm, the curves at 20 and 10 nm both show a downward inflection at equal intensity. At 600/570 nm a pattern is not evident. Although there is an inflection at the smallest wavelength interval, the bird had developed such a strong response bias that very few responses were being made to the "different" key and thus this curve represents a very small sample of responses. The same is true for the one curve obtained at .2 log unit intensity difference.

Figure 12.

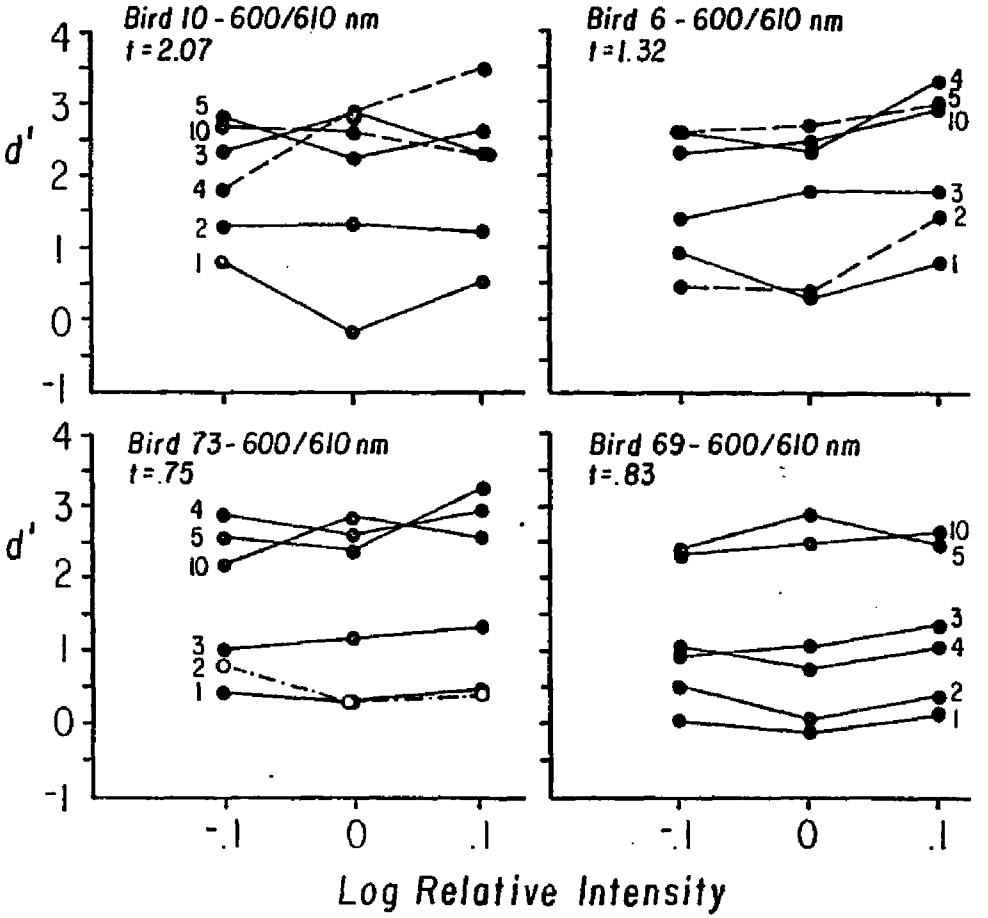
Intensity-wavelength interactions for normal birds comparing 600 nm with longer wavelengths. On the vertical axis is sensitivity, scaled in terms of d' (the method of deriving d' is discussed in the text). On the horizontal axis is log relative intensity, with the more intense stimulus on the right and the less intense stimulus on the left. The small numbers next to each function represent the interval in nanometers of the wavelength discrimination in each case. The t value for the planned comparisons (described in the text) are shown on the graph for each bird.

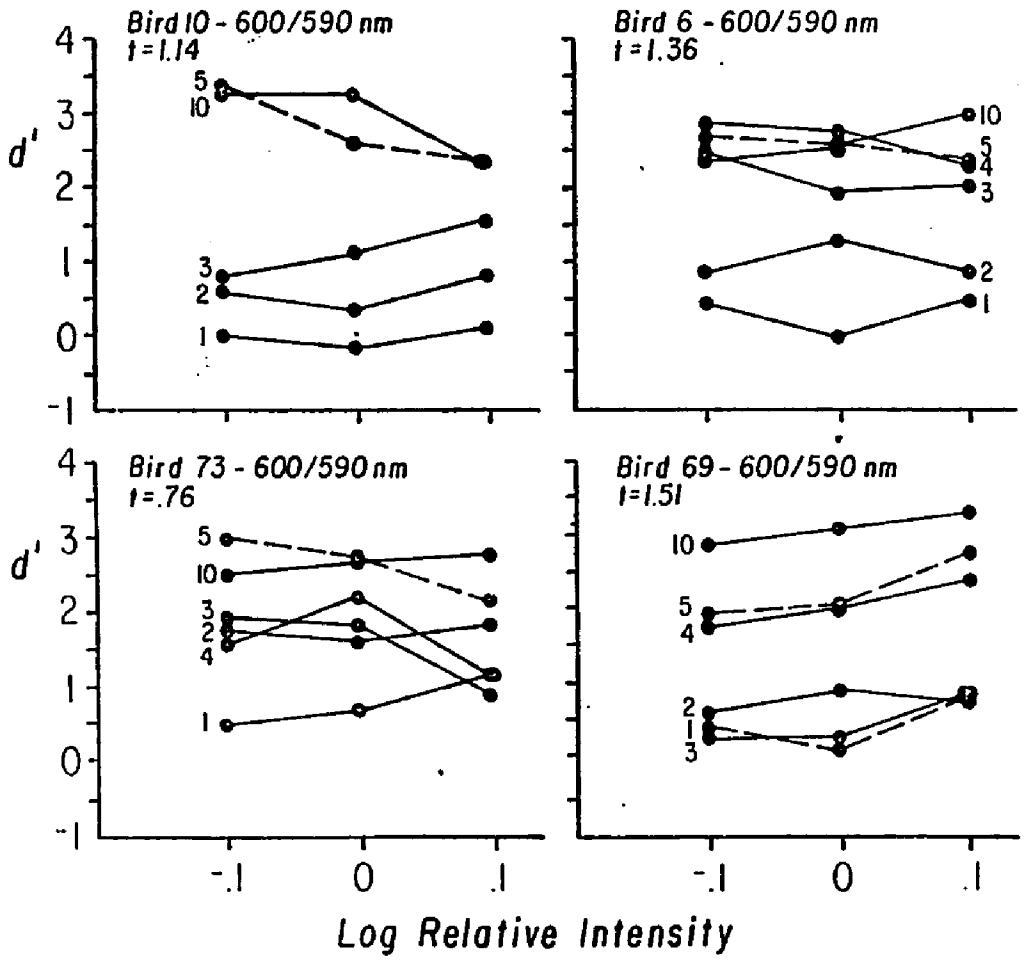
Figure 13.

Intensity-wavelength interactions for normal birds comparing 600 nm with shorter wavelengths. Axes as in Figure 12.

Figure 14.

Intensity-wavelength interactions for Birds 69 and 73 when the standard stimulus was 600 nm and the intensity interval was .2 log unit. Axes is in Figure 12.


Bird 10 - 600/610 nm
t = 2.07
Bird 6 - 600/610 nm
t = 1.32
Bird 73 - 600/610 nm
t = .75
Bird 69 - 600/610 nm
t = .83
d'
4
3
2
1
0
-1
5
10
3
4
2
1
-.1
0
.1
Log Relative Intensity


Bird 10 - 600/590 nm
t = 1.14
Bird 6 - 600/590 nm
t = 1.36
Bird 73 - 600/590 nm
t = .76
Bird 69 - 600/590 nm
t = 1.51
d'
4
3
2
1
0
-1
-.1
0
.1
Log Relative Intensity

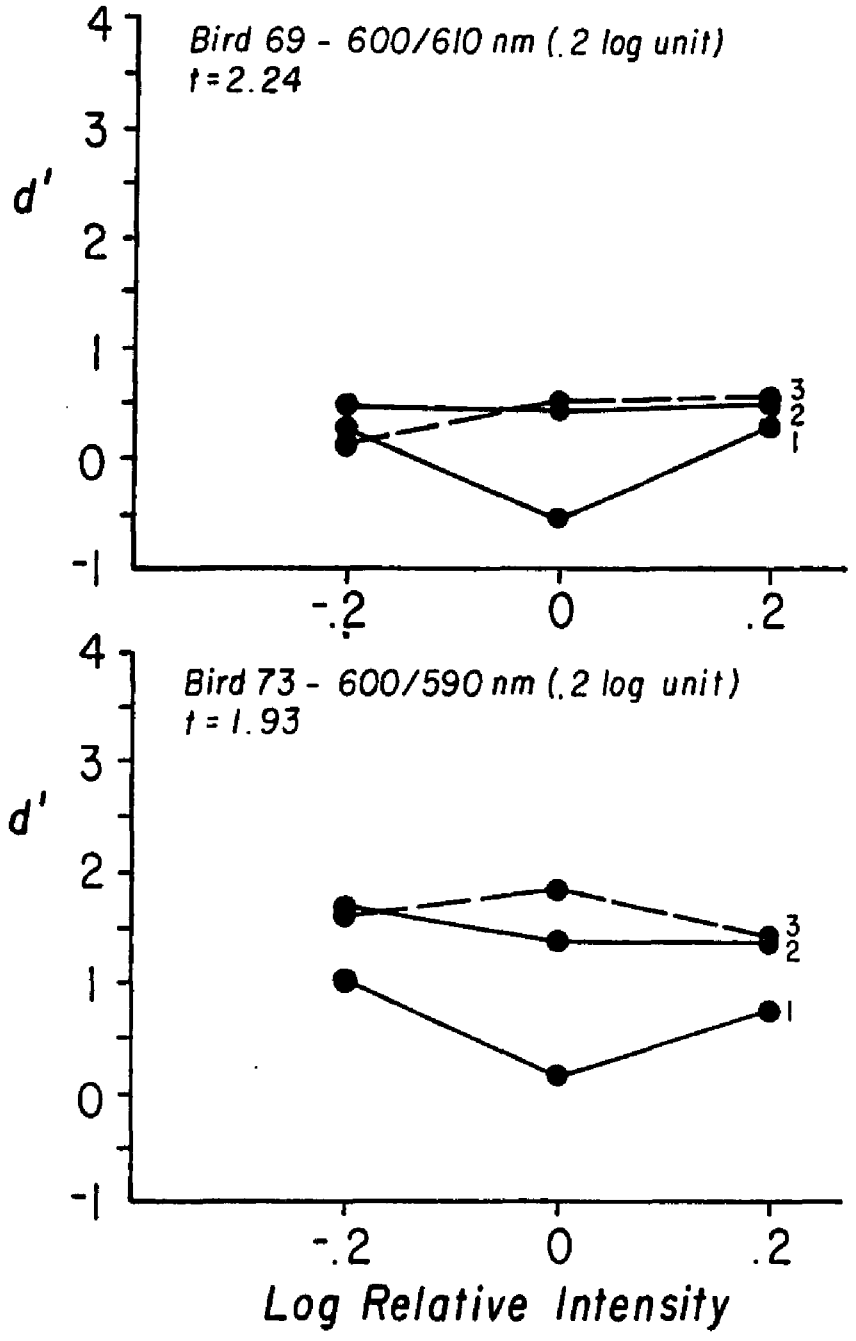
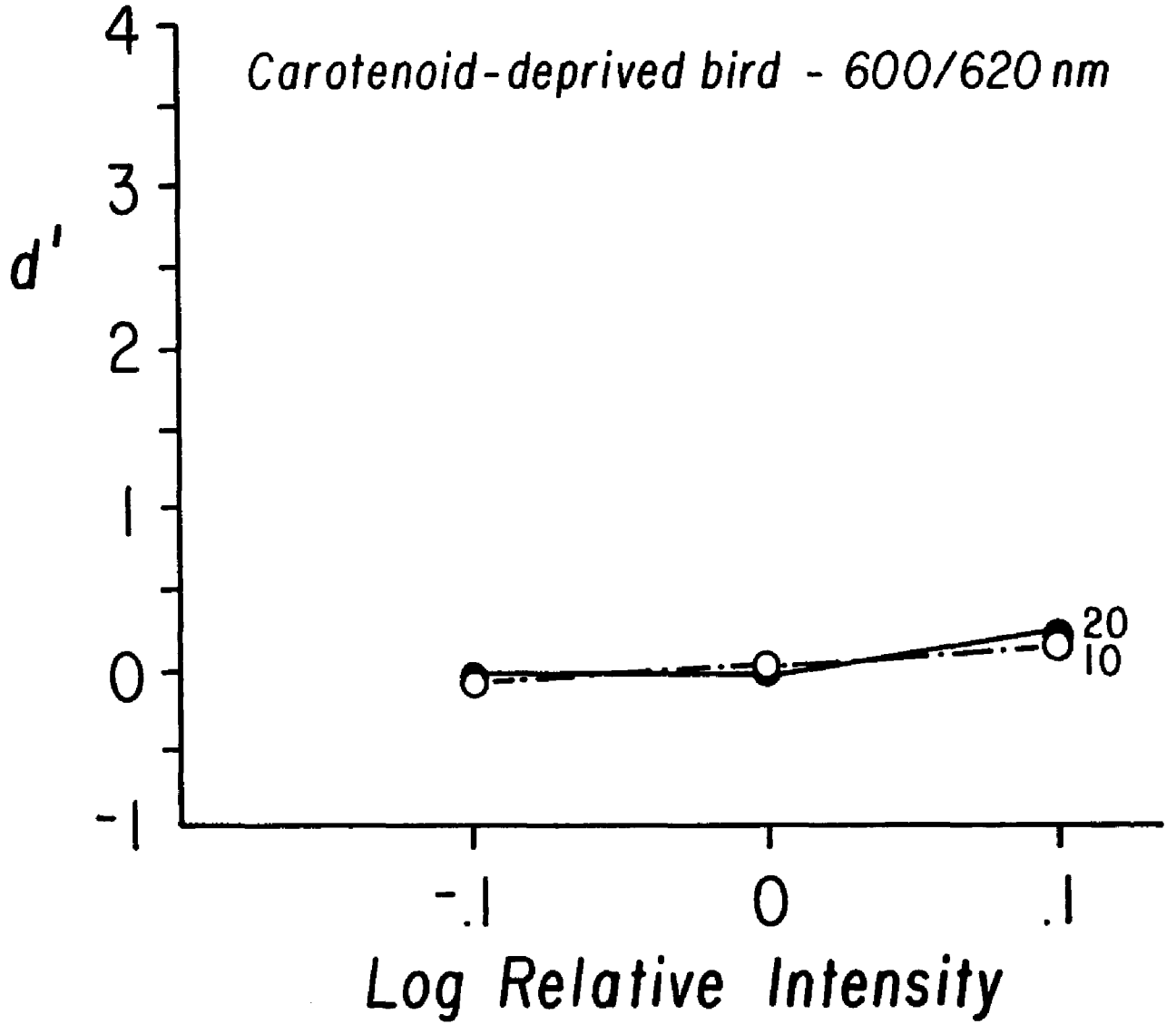

Bird 69 - 600/610 nm (.2 log unit)
t=2.24
d'
4
3
2
1
0
-1
-.2
0
.2
3
2
1
Bird 73 - 600/590 nm (.2 log unit)
t = 1.93
d'
4
3
2
1
0
-1
-.2
0
.2
3
2
1
Log Relative Intensity

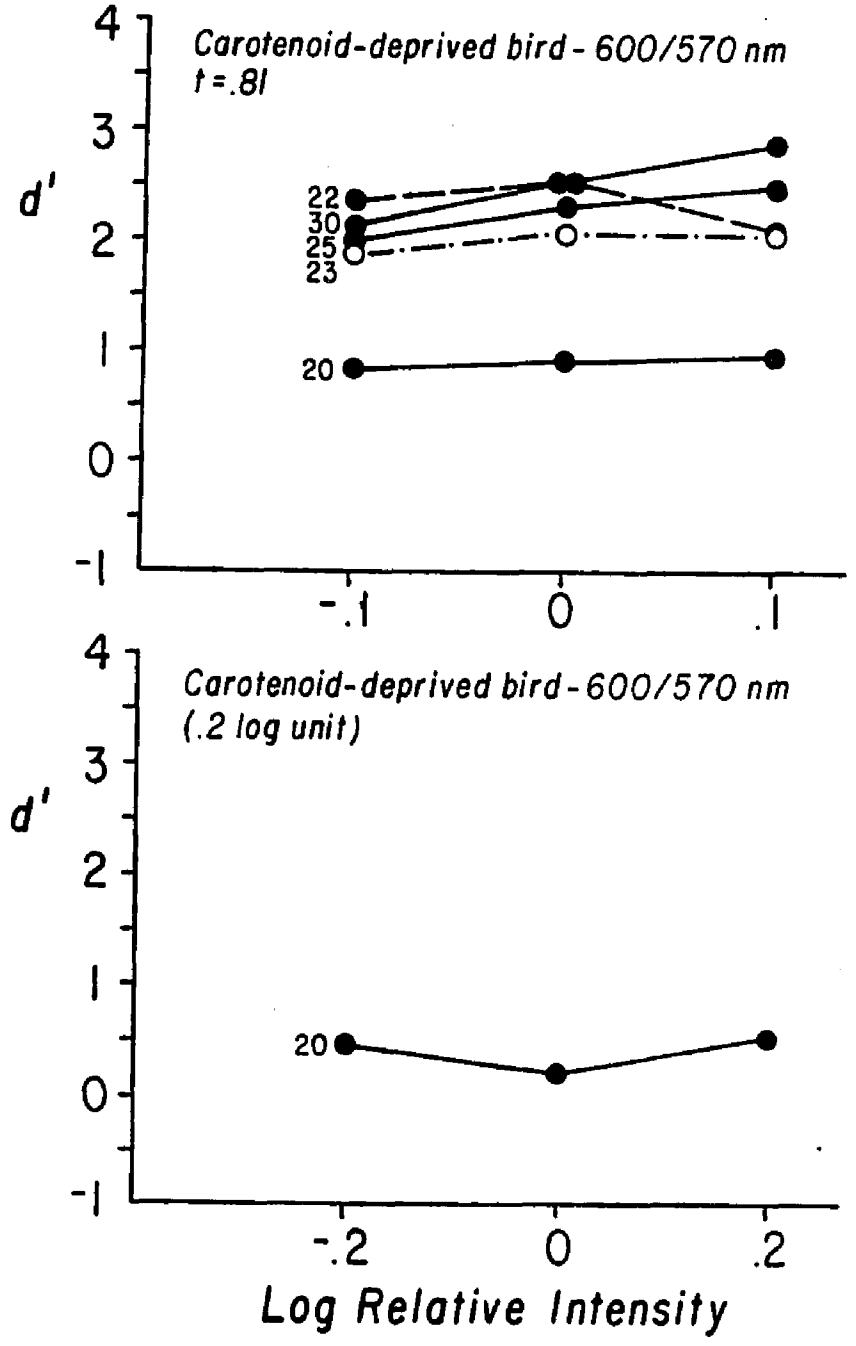
Figure 15.

Intensity-wavelength interactions for the carotenoid-deprived bird comparing 600 and longer wavelengths. On the vertical axis is sensitivity, scaled in terms of d'. On the horizontal axis is log relative intensity, with the more intense stimulus on the right and the less intense stimulus on the left. The small numbers next to each function represent the interval in nanometers of the wavelength discrimination in each case.

Figure 16.

Intensity-wavelength interactions for the carotenoid-deprived bird comparing 600 and shorter wavelengths (.1 and .2-log unit intervals). Axes as in Figure 15.


Carotenoid-deprived bird - 600/620 nm
d'
4
3
2
1
0
-1
-.1
0
.1
Log Relative Intensity
20
10


Carotenoid-deprived bird - 600/570 nm
t = .81
d'
4
3
2
1
0
-1
22
30
25
23
20
-.1
0
.1
Carotenoid-deprived bird - 600/570 nm
(.2 log unit)
d'
4
3
2
1
0
-1
20
-.2
0
.2
Log Relative Intensity

Figures 17 through 19 show the performance of Birds 6 and 69 at 500 nm. The results are not as clearcut as for 600 nm. For Bird 6 at 500 nm versus shorter wavelengths, there seems to be no definite pattern of responding to intensity information with a .1-log increment, even at very small wavelength intervals, but the V-shaped curve appears when a .2-log increment is introduced at a 4-nm wavelength interval, shown in Figure 18. For Bird 6 at 500/520 nm (Fig. 19), there does appear to be some evidence of responding to a .1-log intensity increment, starting at a 9-nm interval; responding seems actually to be less consistent when a .2-log increment is used. No pattern of responding appears for Bird 69 at either intensity.

Figures 20 through 22 show the curves of Birds 10 and 73 at 560 nm. Both the 560/540 nm and 560/580 nm response curves seem to indicate that Bird 10 was responsive to intensity at most wavelength intervals tested. Although in some cases performance was poorer at the lower intensity than at equal intensity, in all cases but one (15-nm interval at 560/580 nm) performance was best at the highest intensity. This response pattern is intensified with a .2-log-unit intensity difference (Fig. 21). For Bird 73 the pattern is less clear, although the V-shaped curves do appear at the three smallest wavelength intervals (16, 15, and 13 nm) with a .1-log intensity difference; with a .2-log-unit difference (Fig. 21) the improvement in performance at higher and lower intensities, and the

Figure 17.

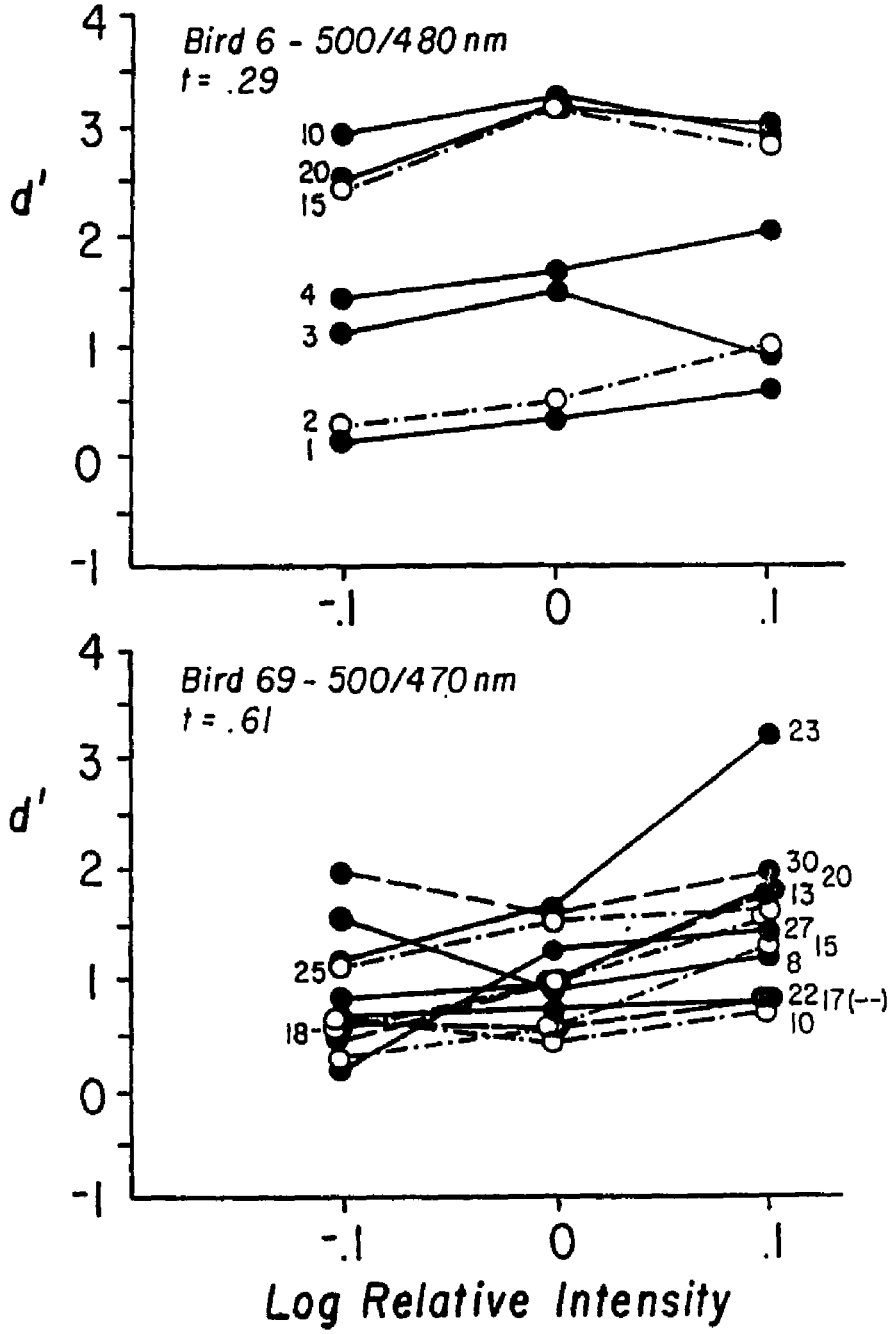
Intensity-wavelength interactions for Birds 6 and 69 comparing 500 nm and shorter wavelengths. On the vertical axis is sensitivity, scaled in terms of $d'$. On the horizontal axis is log relative intensity, with the more intense stimulus on the right and the less intense stimulus on the left. The small numbers next to each function represent the interval in nanometers of the wavelength discrimination in each case. The t values for the planned comparisons are shown on the graph for each bird.

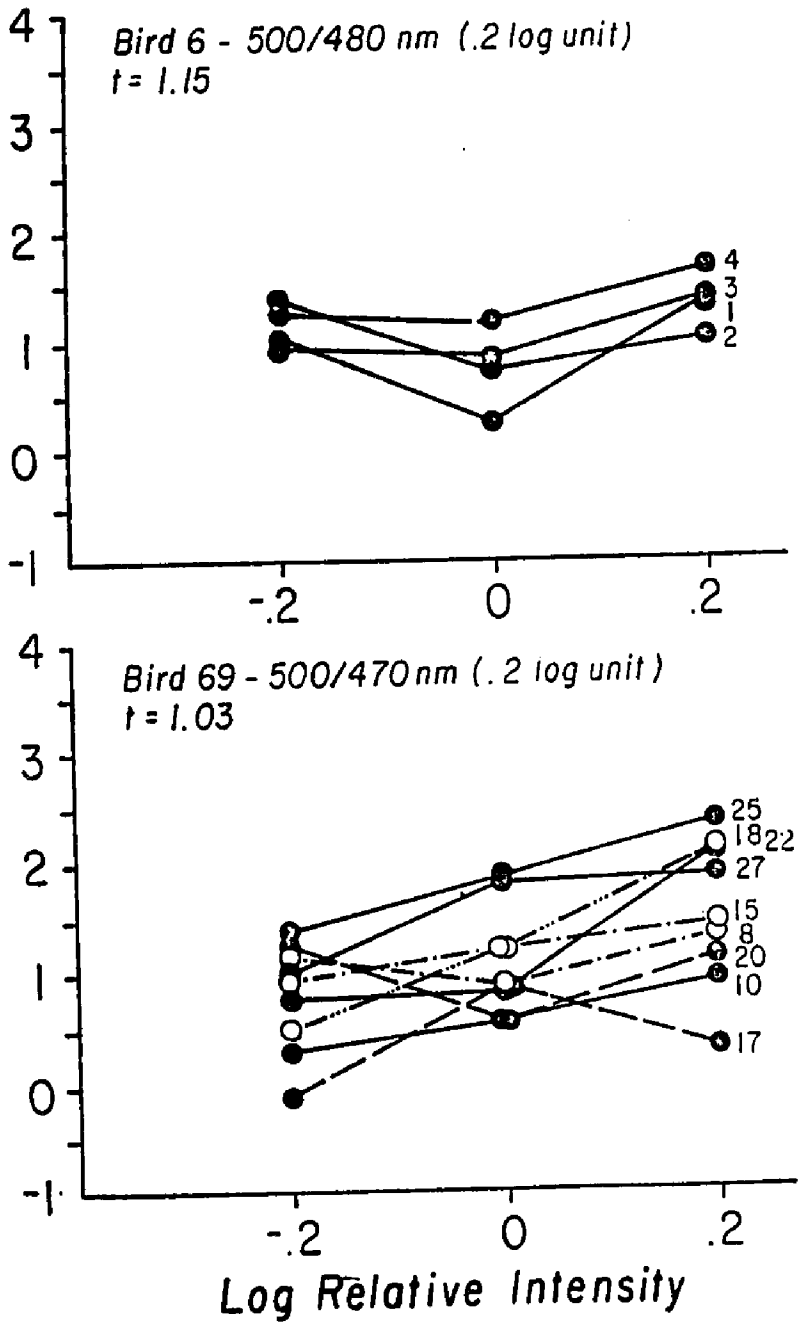
Figure 18.

Intensity-wavelength interactions for Birds 6 and 69 comparing 500 nm and shorter wavelengths when the intensity interval was .2 log unit. Axes as in Figure 17.

Figure 19.

Intensity-wavelength interactions for Bird 6 comparing 500 and longer wavelengths (.1- and .2-log-unit intervals). Axes as in Figure 17.


Bird 6 - 500/480 nm
t = .29
d'
4
3
2
1
0
-1
10
20
15
4
3
2
1
-.1
0
.1
Bird 69 - 500/470 nm
t = .61
d'
23
30
20
13
27
15
8
25
22
17(--)
10
18
Log Relative Intensity


Bird 6 - 500/480 nm (.2 log unit)
t = 1.15
4
3
2
1
0
-1
-.2
0
.2
4
3
1
2
Bird 69 - 500/470 nm (.2 log unit)
t = 1.03
4
3
2
1
0
-1
-.2
0
.2
25
18
22
27
15
8
20
10
17
Log Relative Intensity

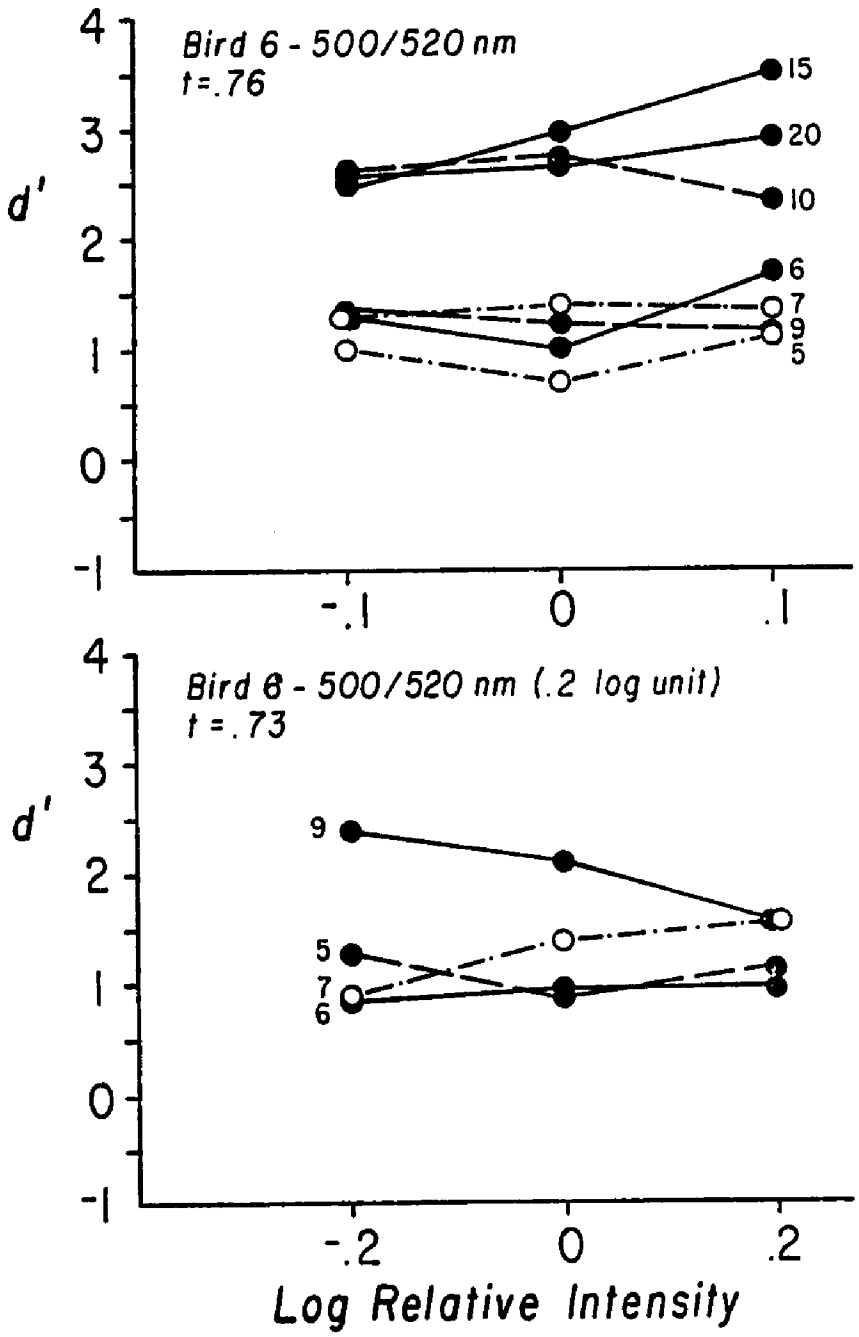

Bird 6 - 500/520 nm
t=.76
d'
4
3
2
1
0
-1
15
20
10
6
7
9
5
-.1
0
.1
Bird 6 - 500/520 nm (.2 log unit)
t = .73
d'
9
5
7
6
-.2
0
.2
Log Relative Intensity

Figure 20.

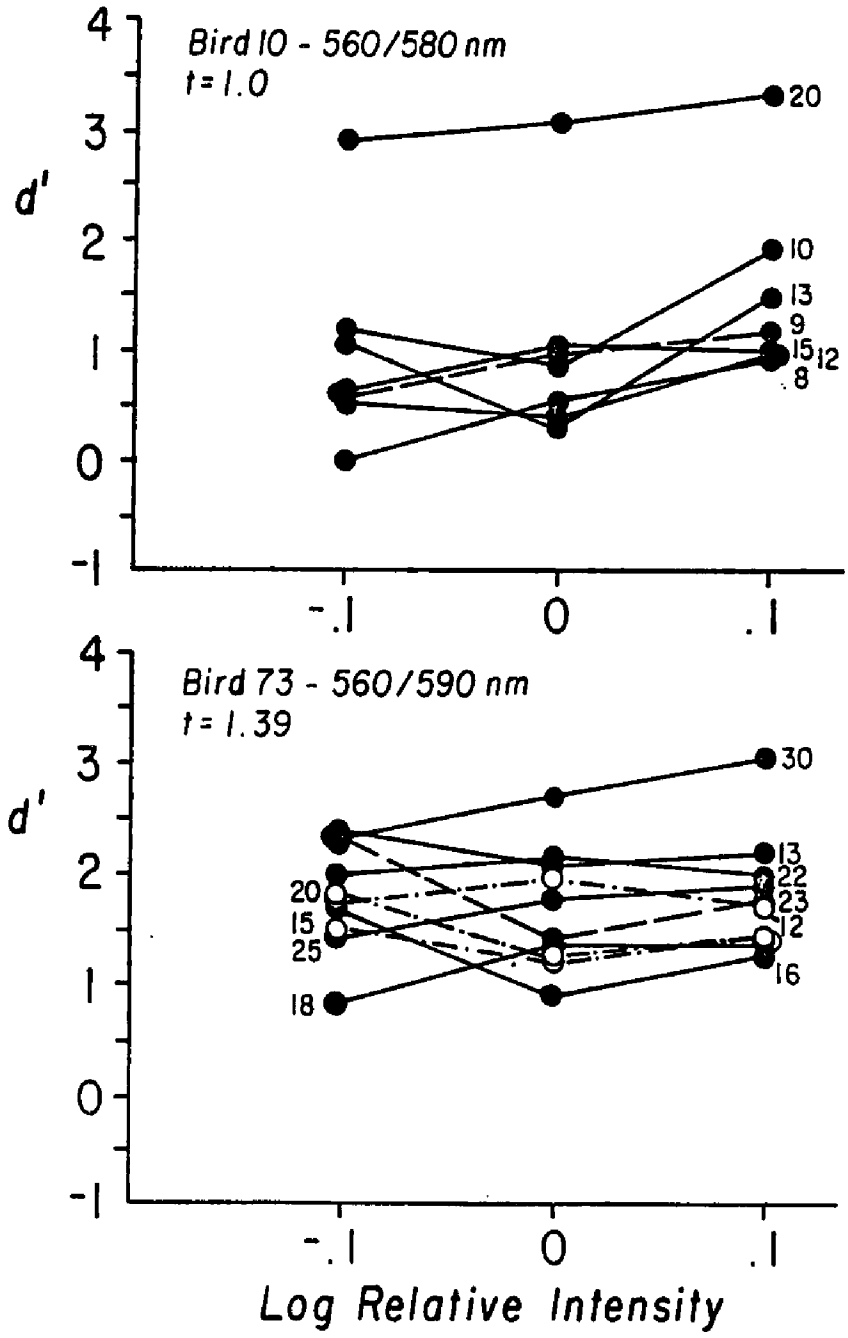
Intensity-wavelength interactions for Birds 10 and 73 comparing 560 and longer wavelengths. On the vertical axis is sensitivity, scaled in terms of $d'$. On the horizontal axis is log relative intensity, with the more intense stimulus on the right and the less intense stimulus on the left. The small numbers next to each function represent the interval in nanometers of the wavelength discrimination in each case. The t value for the planned comparison is shown on the graph for each bird.

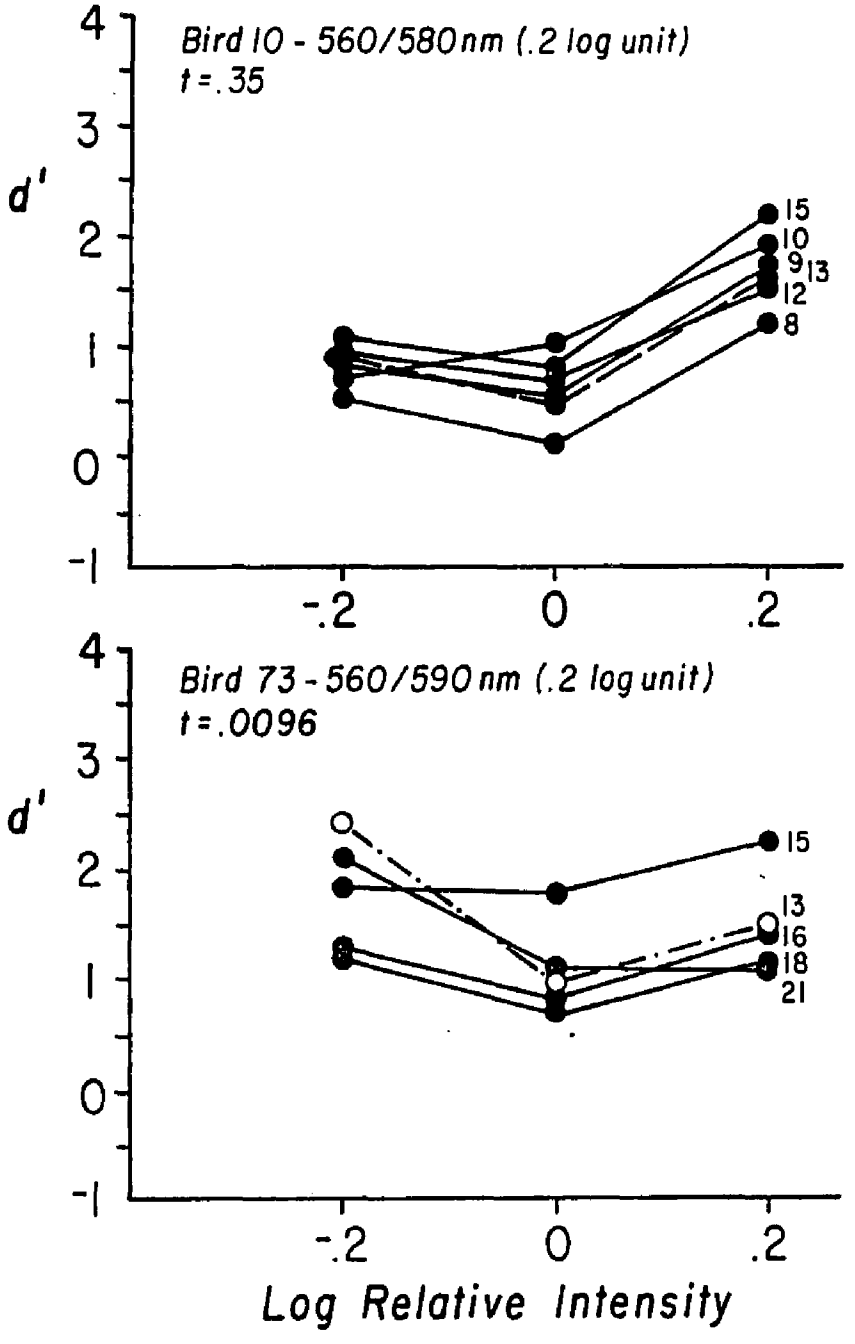
Figure 21.

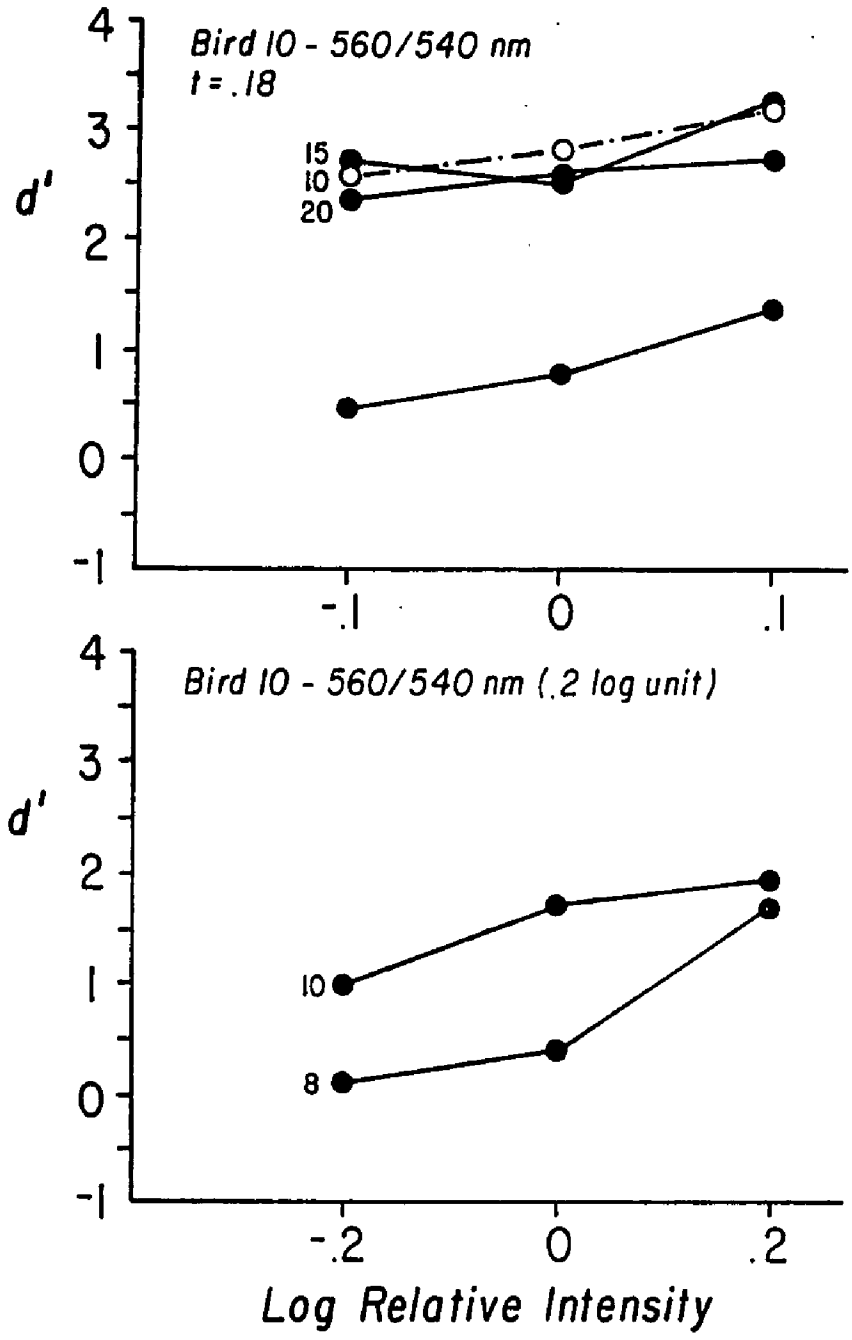
Intensity-wavelength interactions for Birds 10 and 73 comparing 560 and longer wavelengths when the intensity interval was .2 log unit. Axes as in Figure 20.

Figure 22.

Intensity-wavelength interactions for Bird 10 comparing 560 and shorter wavelengths (.1- and .2-log unit interval). Axes as in Figure 20.


Bird 10 - 560/580 nm
t = 1.0
d'
4
3
2
1
0
-1
20
10
13
9
15
12
8
-.1
0
.1
Bird 73 - 560/590 nm
t = 1.39
d'
4
3
2
1
0
-1
30
13
22
23
12
16
20
15
25
18
-.1
0
.1
Log Relative Intensity


Bird 10 - 560/580nm (.2 log unit)
t=.35
d'
4
3
2
1
0
-1
-.2
0
.2
15
10
9
13
12
8
Bird 73 - 560/590 nm (.2 log unit)
t=.0096
d'
4
3
2
1
0
-1
-.2
0
.2
15
13
16
18
21
Log Relative Intensity


Bird 10 - 560/540 nm
t = .18
d'
4
3
2
1
0
-1
15
10
20
-.1
0
.1
Bird 10 - 560/540 nm (.2 log unit)
d'
4
3
2
1
0
-1
10
8
-.2
0
.2
Log Relative Intensity

deterioration in performance at equal intensity, is more obvious.

Planned comparisons were also applied to these discriminations at wavelengths other than 600 nm; t's are shown on each graph. Comparisons in each case were made between performance at the smallest wavelength interval tested and all others combined. None were significant and most did not approach significance. A statistic appropriate for comparing performance at 600 nm and other wavelengths could not be found because the wavelength intervals used were not the same at 600 nm and other spectral regions.

To try to determine whether the negative-going d' scores at small wavelength intervals represented a response strategy on the part of the birds, or were just a consequence of chance-level responding, a computer simulation of a bird responding randomly was run. Random responding on this two-choice procedure centered around a 50% (chance) level of correct responding. Negative d' scores of similar magnitude to those produced by the real birds were generated by the simulation, indicating that these negative scores do not represent "purposive" responding.

## Intensity discrimination

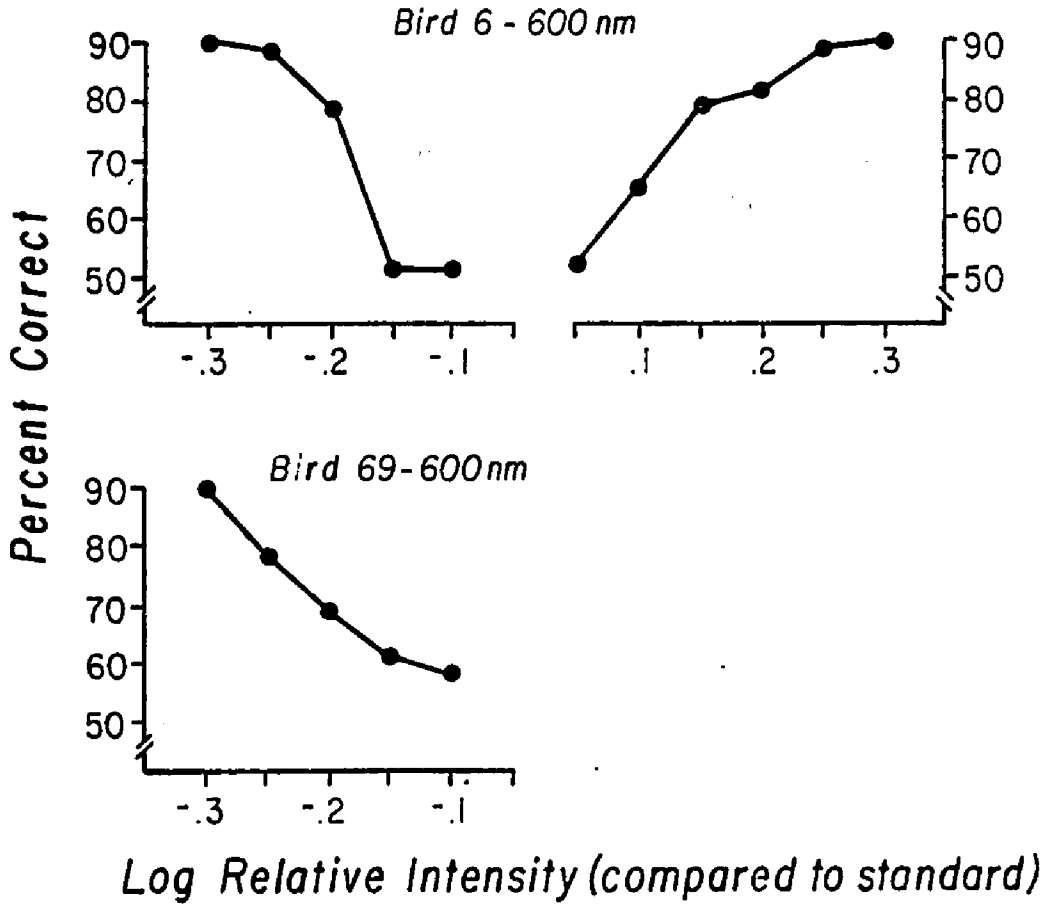
The data for the intensity discrimination are plotted in Figure 23. Bird 6 performed better when comparing the standard intensity to a more intense one: threshold (75% correct) was maintained until .13 log unit, compared with .1875 log unit when comparing the standard with a less intense light. Bird 69 reached threshold at .23 log unit. Because the single discrimination (equal/less intense) by Bird 69 took so long to obtain, the equal/more intense discrimination was not attempted.

Weber fractions were computed for these discriminations, as suggested by Hodos and Bonbright (1972). At difference threshold, the Weber fraction for Bird 6 comparing the standard intensity to a lower intensity was .35; when the standard was paired with higher intensities the Weber fraction was .26. For Bird 69 comparing the standard to lower intensities the Weber fraction was .41. The intensity of the standard stimulus was .24 $cd/m^2$.

The intensity discrimination at 600 nm was learned only with great difficulty and only by two of the normal birds. Attempts lasting six months produced no better than chance responding from one of the other normal birds; the fourth normal bird's performance was extremely variable, ranging from near criterion to 75% correct responding, often on successive days. Several months of training the carotenoid-deprived bird produced only chance levels of

Figure 23.

Intensity-only discrimination for Birds 6 and 69 when wavelength was set at 600 nm. On the vertical axis is sensitivity, scaled in terms of percent correct. On the horizontal axis is the log relative intensity of each stimulus compared to the intensity of the standard stimulus.


Bird 6 - 600 nm
Bird 69 - 600 nm
Percent Correct
90
80
70
60
50
-.3
-.2
-.1
.1
.2
.3
Log Relative Intensity (compared to standard)

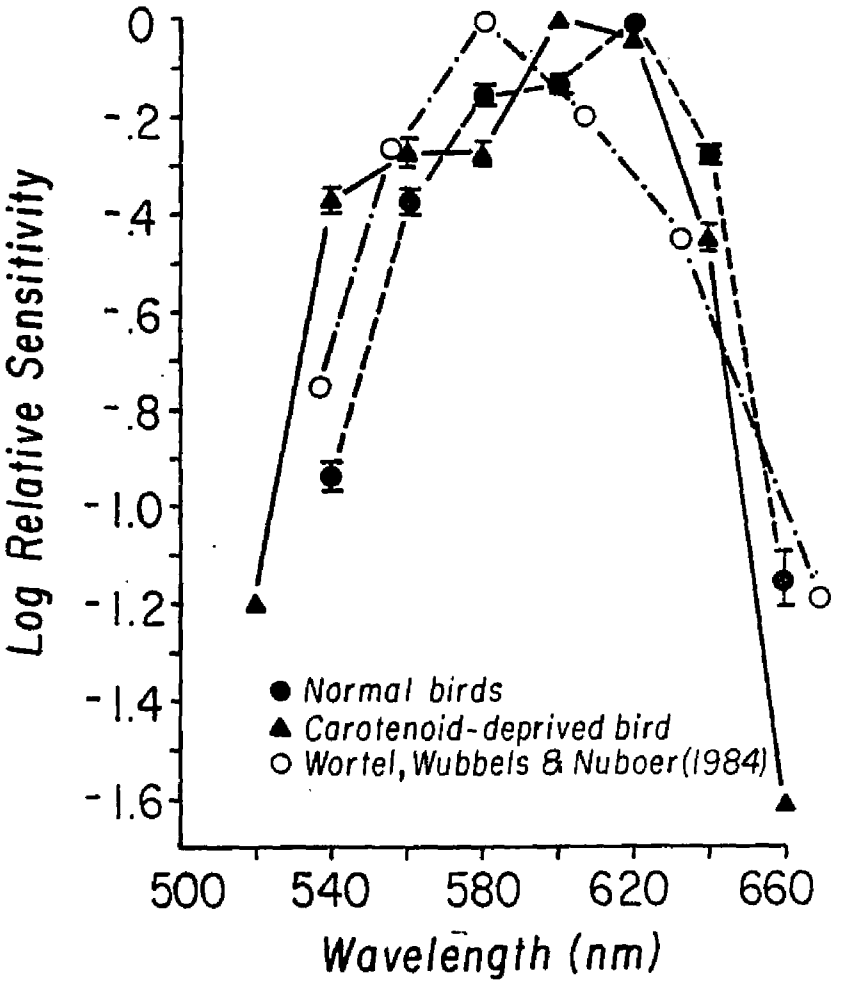
correct responding. An attempt to teach Birds 6 and 69 to discriminate intensity differences when both halves of the split key were lit with 500-nm light was wholly unsuccessful. Bird 69 never showed any mastery of the discrimination, and Bird 6, while occasionally, after many months of training approaching criterion, never reached it, and began to show increasing signs of agitation at the prospect of being placed in the chamber.

## Electroretinography

In order to derive relative spectral sensitivity curves, response amplitude was measured for each intensity at each wavelength. Amplitude as a function of intensity was plotted, then the best straight line was fitted (by eye) to all functions. Relative sensitivity was determined by horizontally sliding the function for each wavelength to fit the one which yielded the maximum sensitivity. The magnitude of the horizontal shift for each wavelength was the relative spectral sensitivity. Results of the ERG experiments with two normal and the experimental birds are shown in Figure 24. The peak sensitivity for the normal birds is at 620 nm, with sensitivity falling off steeply at longer wavelengths, and somewhat less steeply at shorter wavelengths. The function for the carotenoid-deprived bird indicates that sensitivity at wavelengths above 620 nm

Figure 24.

Electroretinograph results for the carotenoid-deprived and two normal birds. The axes show log relative sensitivity as a function of wavelength. Brackets above and below each data point represent the standard error of the mean. Method for deriving the spectral sensitivity curve is described in the text. Shown for comparison are the red field flicker ERG data of Wortel, Wubbels, & Nuboer (1984).


0
-.2
-.4
-.6
-.8
-1.0
-1.2
-1.4
-1.6
Log Relative Sensitivity
500
540
580
620
660
Wavelength (nm)
Normal birds
Carotenoid-deprived bird
Wortel, Wubbels & Nuboer (1984)

decereased even more precipitously that for the normal birds, while sensitivity at 560 and 540 nm was elevated considerably above that of the normal birds. Maximum sensitivity for this bird was displaced to 600 nm.

Included on the graph for comparison are flicker ERG red field results of Wortel, Wubbels, and Nuboer (1984). Sensitivity at 540 and 560 nm, and at wavelengths above 600 nm, are similar for their birds and for the normal birds in this study. Sensitivity peaks at shorter wavelengths in their study, but sensitivities at 580-600 nm are not dissimilar from those for the normal birds in this study. Major differences are evident between their results at 540 and 660 nm and those of the carotenoid-deprived bird at those wavelengths; sensitivity for the deprived bird at 540 nm is elevated considerably above that of the birds in the Wortel, Wubbels, and Nuboer study, while at 660 nm, the carotenoid-deprived bird's sensitivity has fallen below that of the birds in that study.

Flicker responses for the normal and carotenoid-deprived birds were similar in amplitude and waveform.

## Histology

A photomicrograph of the retina of the control bird is shown in Figure 25. The red, orange, yellow, and yellow-green droplets are all evident. The retina of the carotenoid-deprived bird is shown in Figures 26 and 27. In

Figure 26, normal-appearing orange, yellow, and yellow-green droplets are evident. In Figure 27, however, the large empty vacuoles indicate that the red pigment was absent.

The retina of the newly hatched squab is shown in Figure 28. All droplets appear to be unpigmented.

The anatomical study of the retina using light microscopy indicated that the retina of the carotenoid deprived bird was healthy, and indistinguishable from that of the normal bird.

Figure 25.

Photomicrographs of flatmount of unstained, unfixed retina of normal bird, showing pigmented oil droplets. Scale is shown under photos.

Figure 26.

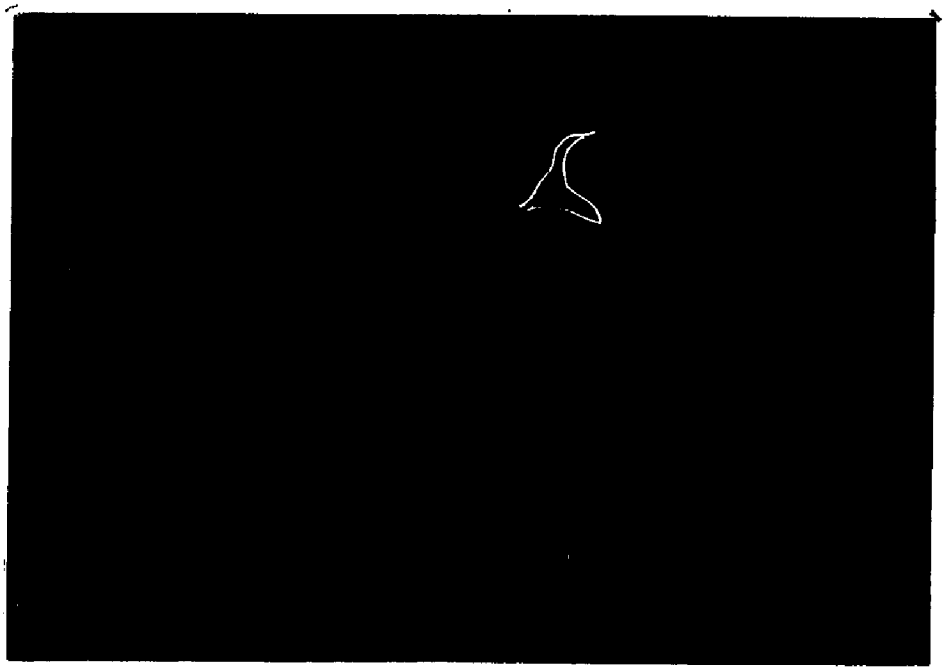
Photomicrographs of flatmount of unstained, unfixed retina of carotenoid-deprived bird, showing oil droplets with orange and yellow droplets. Scale is shown under photos.

Figure 27.

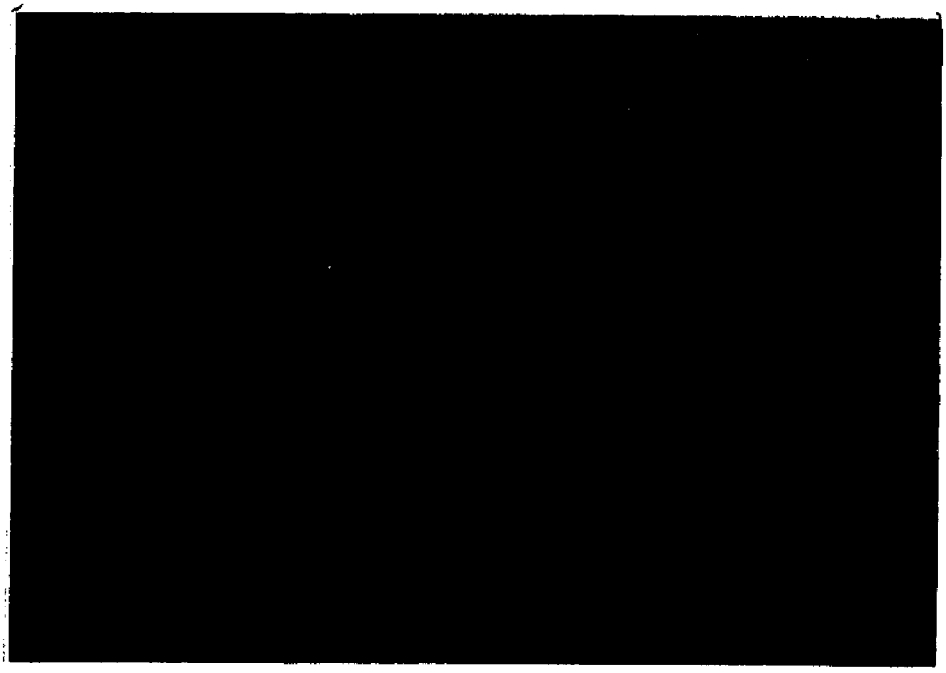
Photomicrographs of flatmount of unstained, unfixed retina of carotenoid-deprived bird, showing unpigmented vacuoles normally filled with red pigment. Scale is shown under photos.

Figure 28.

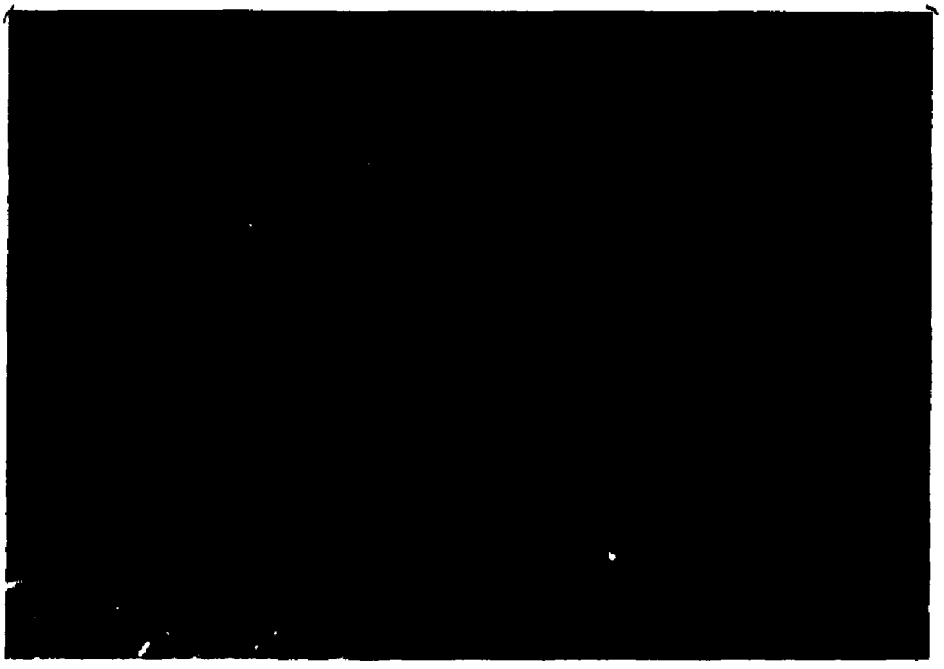
Photomicrographs of flatmount of unstained, unfixed retina of carotenoid-deprived bird, showing unpigmented oil droplets. Scale is shown under photos.



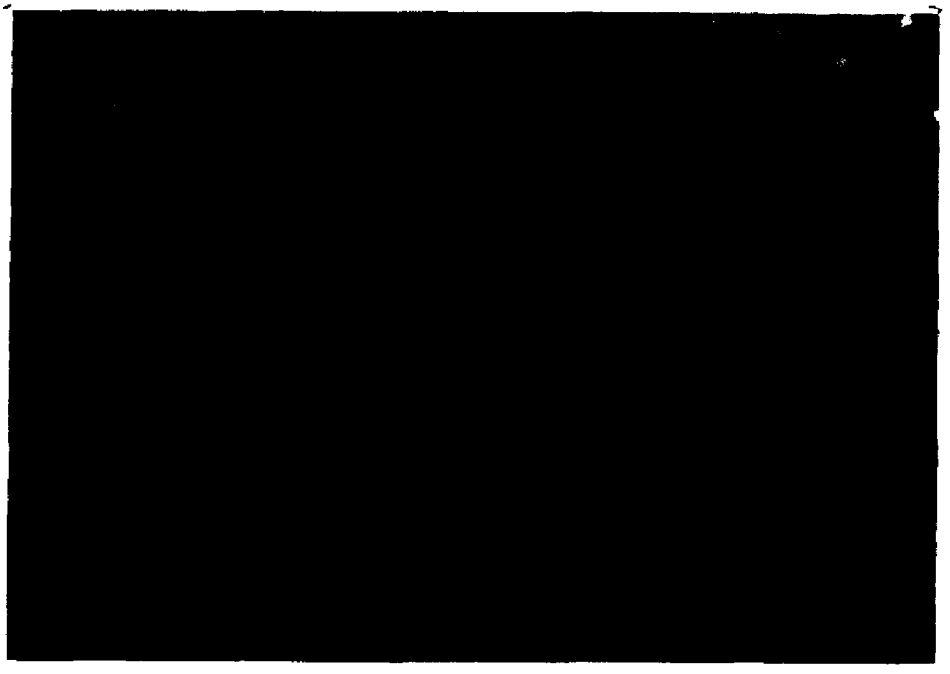
40μ



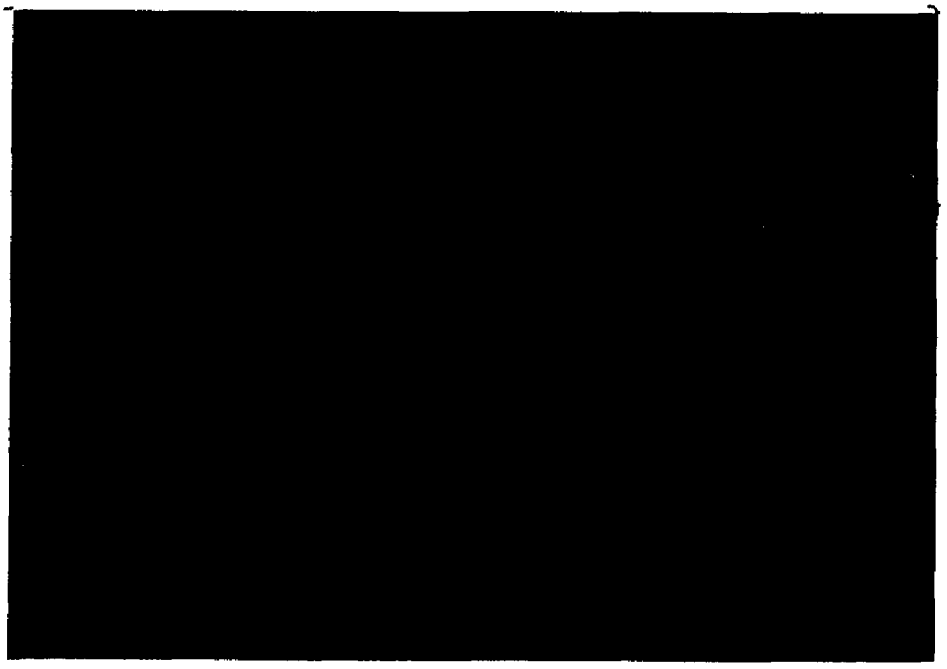
20 μ



40 μ

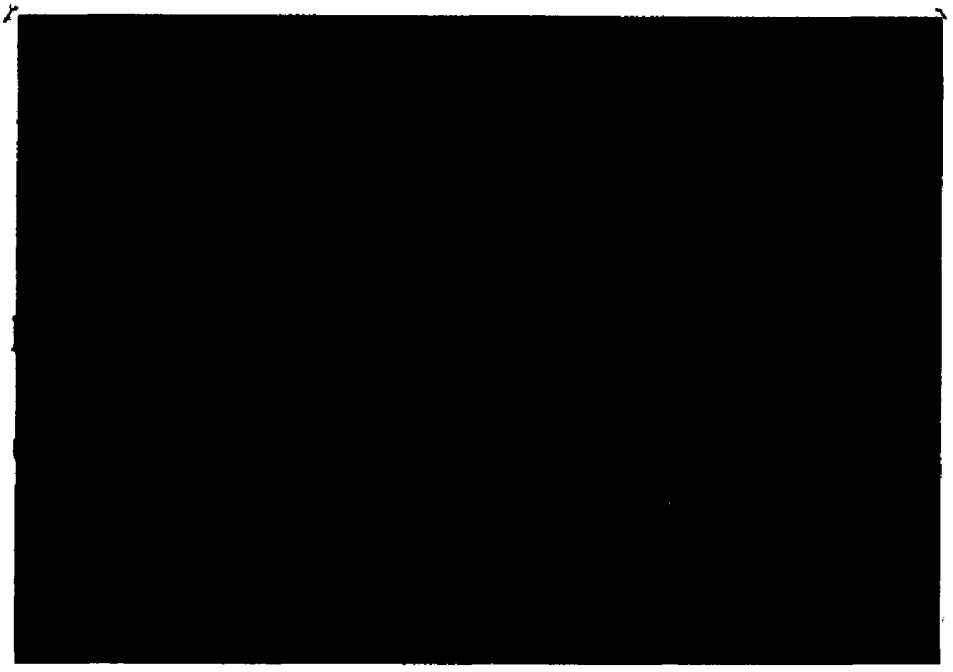


20 μ



40μ

20μ



40 μ

20 μ

## Discussion

The evidence presented here suggests that the red oil droplets do play a role in color vision. The deterioration in performance of the carotenoid-free bird indicates that the droplets contribute to color sensitivity at least at the area aound 600 nm. Droplets other than the red ones still appeared to be present, thus their effect cannot be assessed. How the deficit in color discrimination might manifest itself at other regions of the spectrum remains to be investigated.

If there were any lingering doubt that pigeons discriminate color stimuli on the basis of wavelength rather than intensity, this study should have resolved it. Furthermore, it appears that Donald Blough's (1957) calculation of the point of equal pigeon luminosity is very accurate. When birds responded to intensity at all, higher and lower intensities elicited more correct responses than the stimuli of intensity matched according to Blough.

The negative d' scores produced by the birds probably do not represent a strategic decision by the birds; rather they are a byproduct of chance level responding.

The investigations of the relative salience of intensity and wavelength clearly indicate that pigeons, like humans and old-world monkeys, and unlike cats and ground squirrels, are much more influenced by the wavelength than the intensity component of the visual stimulus. Indeed,

they ignore intensity information until there is virtually no wavelength information available. There is only very slight evidence that the birds responded more to intensity information at spectral areas where their wavelength-discrimination capabilities are less good than they did at the spectral locus of best discrimination.

The intensity discrimination functions yielded by two control birds showed somewhat higher thresholds than those of Hodos and Bonbright (1972). This might be due to differences in procedure: the Hodos and Bonbright study used a successive discrimination procedure rather than a same-different split-key procedure. Also, Hodos and Bonbright used a white light stimulus rather than a monochromatic one and the intensity of their stimuli was greater than that of the stimuli used in this study.

Whether this inability to learn an intensity discrimination is due to a variety of "burnout" (the birds had been performing wavelength discriminations for over two years at the start of intensity training), or whether it is due to the relatively greater salience of the color component of the stimulus is not clear. Nor is it clear why intensity differences at 600 nm should have been more discriminable than at 500 nm. The luminance control procedure hinted that the reverse should have been true - that intensity differences should be more salient at wavelengths other than 600 nm. It is possible that the difficulty in teaching the intensity discriminations was

due to the birds' having learned the wavelength discrimination first. An attempt to train two birds naive with respect to wavelength discrimination on an intensity discrimination was abandoned after several weeks when no sign of learning was evident. A more thorough investigation of this question would be desirable, but it seems that pigeons have difficulty attending to intensity information in the presence of wavelength information.

A fairly recent and burgeoning literature on pigeon cognitive processes suggests that the same-different procedure was an ineffective paradigm for studying color discrimination in these animals. There is a growing consensus that pigeons can form abstract "concepts" under certain circumstances, and there is beginning to be some definition of the constraints on concept formation. Lombardi, Fachinelli, and Delius (1984), for example, proposed that number of examples might determine whether pigeons were able to develop a given concept: giving more exemplars of a certain concept might facilitate learning. They found that while acquisition of an oddity task was slower for pigeons given a larger set of examples, transfer of learning to novel stimuli was slightly better than for birds given fewer examples. Performance to novel stimuli was never as good as for training stimuli, indicating that concept learning was imperfect. Of interest to the present study is the authors' observation that "color stimuli may be inadequate to demonstrate concept formation because of

their exceptional salience and memorability" (p.6).

A study by Nelson and Wasserman (1981) bears on this question. They tested pigeons on a delayed conditional discrimination: a sample stimulus was presented and, after a delay, a test stimulus. For each sample, only one test stimulus was paired with reinforcement. Performance during the test provided evidence of memory for the sample. Stimuli were pairs of colors and line tilts, with colors the sample stimuli for one group, and line tilts the sample for the other. Nelson and Wasserman found that when the color was the sample and line orientations were test stimuli the birds learned the task easily; in the reverse condition, the birds did not learn at all. When the study was repeated using a within-subject design, the same birds who were easily able to earn the color-as-sample condition performed at chance levels when the line tilts were samples. The authors suggest that line stimuli are not so well remembered as color stimuli.

Herrnstein (1985) has recently reported studies that show that pigeons find it very easy to recognize exemplars of such categories as bodies of water, for example, but that they are inept at relational discriminations (such as same/different tasks): "pigeons learn only with some trouble that they are being reinforced for responding to a stimulus that matches another stimulus in some respect, or that does not match it. When they do learn to solve such problems, they do so with less generality than they could,

as if the abstract relation of identity or difference is contaminated by the specific stimulus features of the stimuli used to illustrate it" (p. 138).

This evidence suggests that a split-key, same-different paradigm is far from ideal for the type of problem under investigation in the present study. If I were to repeat this study, I would use a go/no-go, stimulus-annulus paradigm, where the stimulus and annulus could vary in wavelength and/or intensity, and the bird would be reinforced for pecking when a difference was present, and refraining from pecking when there was no difference. This would not solve the problem of lack of generality of color stimuli *per se*, but if acquisition were quicker, retraining to each novel stimulus would be less troublesome.

It would have been desirable to have tested additional carotenoid-deprived birds, but the invariability of the performance of the normal birds at 600 nm, and the relatively large deviation in performance of the experimental bird, seem to justify the conclusion that this bird had a large color discrimination deficit. In addition, the ERG data provide some evidence that only the oil droplets, and not the cones, were affected by the carotenoid-free diet. The slight V-shaped inflection at 600/570 and .2 log unit also suggest that the bird responded typically to intensity in the presence of wavelength, suggesting that other retinal elements were not affected. The abrupt and steep fall off in sensitivity

above 620 nm is consistent with both theoretical models (e.g., Bowmaker, 1979) and the finding that the carotenoid-deprived bird was unable to discriminate wavelength differences above 600 nm. The elevated sensitivity at 540 and 560 nm is also to be expected from droplet-cone relationships (Bowmaker, 1979). It is somewhat surprising that sensitivity is so high at 600 and 620 nm. A number of possibilities suggest themselves to explain this. First, although no red droplets were seen on microscopic examination, some may have retained their pigmentation. The entire retina was not examined, since some could not be detached from the pigment epithelium. A likelier possibility is that the orange and yellow droplets, which were still present, acted to shift effective $\lambda$max of their cone pigments to longer wavelengths. It is also possible that an undetected cone pigment with $\lambda$ max at wavelengths longer than any so far found accounted for the sensitivity at 600 and 620 nm.

The finding that normally reared squabs are hatched without pigmented oil droplets provides an area of future investigation. Histological study of the squab retina should be done to determine at what age the retina is similar to that of the adult; at that age electroretinography could be performed, which would probably give reliable information about color vision capability, since in the adult ERG wavelength-discrimination investigations have yielded

functions not dissimilar in shape from the behavioral functions (Blough, Riggs, & Schaefer, 1972). Behavioral study of color vision in the squab might also be attempted, with some of the response measures used in studying human infants, such as heart and respiration rate. Feather erection might be a useful response measure, since squabs react to novel stimuli by bristling their quills.

Since pigeons do not have pigmented droplets at hatching, it should be possible to investigate the ontogeny and function of the droplets without feeding the birds the manufactured diet, with its attendant expense and peril. This would mean that much larger numbers of carotenoid-free subjects could theoretically be obtained. Parents could be fed a normal grain diet until a week or so before the eggs hatched, and then switched to a carotenoid-free diet of (for instance) white corn for the period of "lactation." Cod liver oil could be given as a supplement. This regimen should be easily supportable for the three weeks during which parents feed their young. Similarly, squabs could be fed this white corn and cod liver oil diet for some period of time, the duration of which would need to be determined experimentally.

The fact that only the red droplets were depigmented suggests that they arise from a different substrate than the other droplets. One possibility is that the parents' crop milk contains a substance sufficient to pigment the orange and yellow droplets. It is possible to hand rear

squabs from hatching, and this should be tried, if a carotenoid-free diet could be devised on which they could survive.

It would also be desirable to rear a bird with depigmented droplets, test behaviorally for color vision deficits, then feed a carotenoid-enriched diet and retest the birds' color vision, as was done by Wallman (1979).

One should not conclude without some speculation about why being able to discriminate orange is important to pigeons. The difficulty in determining the adaptive significance of color vision in general is exaggerated in the case of the pigeon by the fact that, as Martin and Muntz (1979) pointed out, not very much is known about the pigeon as a wild animal. The circumstances that dictated the development of the two retinal fields, for instance, may no longer be relevant to the lives of "feral" pigeons of urban areas. Murton (1965) made a thorough study of the ecology of the wood pigeon (Columba palumba), a species closely related to the rock dove (Columba livia). He found that the bird's diet consisted of clover, grain, tree buds and flowers, and weed seeds, depending on seasonal and local availability. It is striking how dependent on man's agricultural activities the bird's food supply is. What its food sources may have been before its close association with humans began, therefore, is not clear.

The split field is such a distinctive and relatively unusual feature that it invites speculation about its

function. Walls (1942) thought that the yellow field sharpens the contrast of objects seen against the blue sky, by eliminating the sky's color, whereas the red field might heighten contrast of objects seen against a green background. The red field might also eliminate Rayleigh scatter, particularly early in the morning. Walls noted that song birds, most of whom are early risers, have a larger proportion of red droplets than birds active at later hours. For pigeons, at least, this role in elimination of early morning Rayleigh scatter is rendered unlikely by Murton's (1965) observation that the wood pigeon feeds throughout the day, with rate of feeding increasing to a maximum in the late afternoon.

Lythgoe (1971) stated that birds "closely associated with vegetation" (p. 132) have relatively large numbers of red droplets. He noted that the spectral reflectances of green leaves of plants such as dock, mullein, and dogwood are identical below about 550 nm, but diverge subtly at longer wavelengths; red droplets in the red field might thus permit discrimination among these leaves on the basis of their spectral reflectance. Although this information may be available to the pigeon, it is not clear that it is important to it. Goodwin (1983) stated that the rock dove is primarily a seed eater, feeding on ground that is bare or covered only in short vegetation.

What we know about the red field suggests that it is myopic, used to look frontally and downward, most sensitive

at around 600 nm, and best able to discriminate wavelength at that locus. The myopia and frontal vision indicate that the red field is used to locate food at near distances. The sensitivity to long wavelengths combined with its ground-feeding habits tempt one to speculate that the pigeon uses its red field to discriminate reddish-brown seeds from reddish-brown soil.

This study provides support for the idea that one function of the red oil droplets is to sharpen color discrimination, at least at the spectral locus around 600 nm. This relatively small decrement would be missed in a discrimination test like those done with the Japanese quail (Kovach, Wilson, & O'Connor, 1976; Dücker & Schulze, 1977). It might also be less obvious at a different spectral region, where discrimination is less fine. This role in color vision by no means rules out the possibility that the droplets perform other functions; indeed, given the complexity of the droplet-cone relationships, it seems likely that they play a number of roles in vision. It is possible that the droplets compensate for the absence of pigment in the lens and macula, which in other animals serves to screen out unwanted short-wavelength light, thus correcting for chromatic aberration. The droplets may also protect against receptor photooxidation by very short wavelength light. The pigeon has good color discrimination at very short wavelengths as well as at long wavelengths. Thus the pigeon eye cannot have

a "general" filter that screens all incoming light and blocks transmission of ultraviolet light. Some filtering is necessary, however, for reasons suggested above, and the oil droplet-cone dyad system found in the pigeon retina is an effective way of allowing stimulation by very short wavelength light while at the same time protecting the visual system from unwanted consequences of this stimulation.

GENESIS RIVER LABORATORIES DIVISION

1148 Bell Road
Chagrin Falls, Ohio 44022
Phone: (216) 338-5986

Appendix A

## CAROTENOID DEFICIENT PIGEON DIET

### TD83029

| | g/Kg |
|---|---|
| Corn Meal, white, degerminated | 746.0084 |
| Casein,"Vitamin-Free" Test | 113.0 |
| L-Arginine HCl | 5.8 |
| L-Lysine HCl | 3.0 |
| DL-Methionine | 6.0 |
| Cottonseed Oil | 30.0 |
| Fiber (cellulose) | 30.0 |
| Mineral Mix, Fox-Briggs N | 60.0 |
| Choline Chloride | 2.0 |
| Thiamin HCl | 0.015 |
| Riboflavin | 0.015 |
| Calcium Pantothenate | 0.02 |
| Niacin | 0.05 |
| Pyridoxine HCl | 0.006 |
| Folic Acid | 0.005 |
| Biotin | 0.0006 |
| Vitamin $B_{12}$ (0.1% TRituration in Mannitol) | 0.02 |
| Menadione Sodium Bisulfite Complex | 0.003 |
| DL-Alpha Tocopheryl Acetate (1000 U/g) | 0.05 |
| Vitamin A Palmitate (500,000 U/g, dry) | 0.005 |
| Vitamin $D_3$, in sucrose (400,000 U/g) | 0.002 |

This is amended TD 82240 to contain Vitamin A Palmitate

GENESIS RIVER LABORATORIES DIVISION

1148 Bell Road
Chagrin Falls, Ohio 44022
Phone: (216) 338-5986

## Mineral Mix, Fox-Briggs N

| | | g/Kg |
|---|---|---|
| Calcium Carbonate | $CaCO_3$ | 166.6667 |
| Calcium Phosphate, dibasic | $CaHPO_4$ | 473.3333 |
| Cupric Sulfate | $CuSO_4$ | 0.16667 |
| Ferric Citrate | (16.7%) | 3.3333 |
| Magnesium Sulfate | $MgSO_4$ | 50.0 |
| Manganese Sulfate | $MnSO_4 \cdot H_2O$ | 4.16667 |
| Potassium Chloride | KCl | 116.6667 |
| Potassium Iodate | $KIO_3$ | 0.16667 |
| Sodium Chloride | NaCl | 66.6667 |
| Sodium Phosphate, dibasic | $Na_2HPO_4$ | 116.6667 |
| Zinc Carbonate | $ZnCO_3$ | 2.16667 |

Reference: Fox, M.R.S., Briggs, G.M. (1960) J. Nutrion 72, 243-249.

1. Recommended use level in chick diets - 6.0%. This mineral mix also has been used in mouse and guinea pig diets at the same level. However guinea pigs are further supplemented with potassium acetate (25.0 g/Kg) and magnesium oxide (5.0 g/Kg).

## Appendix B. Radiance of Stimuli

I. Radiance of variable and standard stimuli used in behavioral study (value given is for point of equal pigeon luminosity).

Variable Stimulus

| Wavelength | Radiance* | Wavelength | Radiance* |
|---|---|---|---|
| 470 | .25 | 540 | .04 |
| 480 | .16 | 545 | .04 |
| 485 | .17 | 546 | .04 |
| 490 | .08 | 547 | .04 |
| 491 | .15 | 548 | .04 |
| 492 | .15 | 549 | .04 |
| 493 | .16 | 550 | .04 |
| 494 | .16 | 551 | .04 |
| 495 | .13 | 552 | .04 |
| 496 | .13 | 553 | .04 |
| 497 | .14 | 554 | .04 |
| 498 | .14 | 555 | .03 |
| 499 | .14 | 560 | .03 |
| 500 | .11 | 565 | .03 |
| 501 | .11 | 566 | .03 |
| 502 | .11 | 567 | .03 |
| 503 | .11 | 568 | .03 |
| 504 | .11 | 569 | .03 |
| 505 | .10 | 570 | .03 |
| 506 | .10 | 572 | .03 |
| 507 | .10 | 574 | .03 |
| 508 | .10 | 576 | .03 |
| 509 | .10 | 580 | .03 |
| 510 | .09 | 582 | .03 |
| 515 | .10 | 584 | .03 |
| 520 | .10 | 588 | .03 |
| | | 590 | .04 |
| 591 | .04 | 601 | .06 |
| 592 | .04 | 602 | .06 |
| 593 | .04 | 603 | .06 |
| 594 | .05 | 604 | .06 |
| 595 | .06 | 605 | .06 |
| 596 | .06 | 606 | .06 |
| 597 | .06 | 607 | .06 |
| 598 | .06 | 608 | .06 |
| 600 | .06 | 609 | .06 |
| 610 | .06 | 620 | .06 |

Standard Stimulus

| | | | |
|---|---|---|---|
| 500 | .01 | 560 | .0005 |
| 600 | .002 | | |

II. Radiance of stimuli used for electroretinography

| Wavelength | Radiance** Attenuation 0 | .3 | .6 |
|---|---|---|---|
| 520 | 8 | 4 | 2 |
| 540 | 10 | 6 | 2.3 |
| 560 | 12 | 8 | 2.8 |
| 580 | 14 | 8 | 3.2 |
| 600 | 14 | 8 | 3.2 |
| 620 | 14 | 8 | 3.2 |
| 640 | 14 | 8 | 3.2 |
| 660 | 13 | 8 | 3.3 |

*Radiance in mwatt/ster/ft$^2$.
**Radiance in uwatt.

## References

Bloch, S., & Martinoya, C. (1982). Comparing frontal and lateral viewing in the pigeon. I. Tachistoscopic visual acuity as a function of distance. Behavioural Brain Research, 5, 231-244.

Bloch, S., Martinoya, C., & Rivaud,S. (1981). Eye movements in pigeons: participation in binocular fixation and visual pursuit. Journal of Physiology, 320, 20 p.

Blough, D. S. (1957). Spectral sensitivity in the pigeon. Journal of the Optical Society of America, 47, 827-833.

Blough, P.M. (1972). Wavelength generalization and discrimination in the pigeon. Perception and Psychophysics, 12, 342-348.

Blough, P.M. (1979). Functional implications of the pigeon's peculiar retinal structure. In A.M. Granda & J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon (pp. 71-88). New York, Plenum.

Blough, P.M., Riggs, L.A., & Schafer, K.L. (1972).

Photopic spectral sensitivity determined electro-retinographically for the pigeon eye. Vision Research, 12, 477-486.

Bowmaker, J.K. (1977). The visual pigments, oil droplets, and spectral sensitvity in the pigeon. Vision Research, 17, 1129-1138.

Bowmaker, J.K. (1979). Visual pigments and oil droplets in the pigeon retina, as measured by microspectrophotometry and their relationship to spectral sensitivity. In A.M. Granda & J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon. New York: Plenum.

Bridges, C.D.B. (1962). Visual pigments of the pigeon, Columba livia. Vision Research, 2, 125-137.

Brown, J.L., Shively,F.D., LaMotte, P.H., & Sechzer, J.R. (1973). Color discrimination in the cat. Journal of Comparative andPhysiological Psychology, 84, 534-544.

Catania, A.C. (1964). On the visual acuity of the pigeon. Journal of the Experimental Analysis of Behavior, 7, 361-366.

Clayton, K.N., & Kamback, M. (1966). Successful performance by cats on several colour discrimination problems. CanadianJournal of Psychology, 20, 173-182.

Cooper, T.G.& Meyer, D.B. (1968). Ontogeny of retinal oil droplets in the chick embryo (Gallus domesticus) Experimental Eye Research, 7, 434-442.

Cornsweet, T.N. (1970). Visual perception. New York: Academic.

Delius, J.D., Thompson, G., Allen, K.L., & Emmerton, J. (1972). Colour mixing and colour preferences in neonate gulls. Experientia, 28, 1244-1246.

DeValois, K.K., and Switkes, E. (1983) Simultaneous masking interactions between chromatic and luminance gratings. Journal of the Optical Society of America, 73, 11-18.

DeValois, R.L., & Jacobs, G.J. (1971) Vision. In A.M. Schrier & F. Stollnitz (Eds.). Behavior of nonhuman primates: Modern research trends (pp. 107-157). New York: Academic.

DeValois, R.L., & Morgan, H.C. (1974). Psychophysical

studies of monkey vision II. Squirrel monkey wavelength and saturation discrimination. Vision Research, 14, 69-73.

DeValois, R.L., Morgan, H.C., Polson, M.C., Mead, W.R., and Hull, E.M. (1974). Psychophysical studies of monkey vision I. Macaque luminosity and color vision tests. Vision Research, 14, 53-67.

Donovan, W.J. (1978) Structure and function of the pigeon visual system. Physiological Psychology, 6, 403-437.

Doris, J., Casper, M., & Poresky, R. (1967). Differential brightness thresholds in infancy. Journal of Experimental Child Psychology, 5, 522-535.

Dücker, G., & Tiemann, G. (1972). Die Entwicklung der farbigen Ölkugeln in der Retina von Anguis fragilis L., Lacerta agilis L., and Lacerta vivipara Jacq. und ihr Eingluss auf das Farbseh-vermögen. Zeitschrift für Morphologie und Ökologie der Tiere, 71, 105-115.

Dücker, G., & Schulze, I. (1977). Color vision and color preference in Japanese quail (Coturnix

coturnix japonica) with colorless oil droplets. Journal of Comparative and Physiological Psychology, 91, 1110-1117.

Goldsmith, T.H., Collins, J.S., & Light, S. (1984). The cone oil droplets of avian retinas. Vision Research, 24, 1661-1671.

Goodale, M.A. (1983). Visually guided pecking in the pigeon (Columba livia). Brain and Behavior, 22, 22-41.

Goodwin, D. (1983). Pigeons and doves of the world. Ithaca: Cornell University Press, 3rd ed.

Govardovskii, V.I., & Zueva, L.V. (1977). Visual pigments of chicken and pigeon. Vision Research, 17, 537-543.

Graf, V.A. (1979). Four spectral mechanisms in the pigeon (Columba livia). In A.M. Granda & J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon (pp. 129-144). New York: Academic.

Graf, V., and Norren, D.V. (1974). A blue-sensitive mechanism in the pigeon retina: max 400 nm.

Vision Research, 14, 1203-1209.

Guttman, N., & Kalish, H. (1956). Discriminability and stimulus generalization, Journal of Experimental Psychology, 51, 79-88.

Hailman, J.P. (1964). Coding of the colour prefecence of the gull chick. Nature, 204: 710.

Hamilton, W.F., & Coleman, T.B. (1933). Trichromatic vision in the pigeon as illustrated by the spectral hue discrimination curve. Journal of Comparative and Physiological Psychology, 15, 183-191.

Hannover, A. (1840). Über die Netzhaut und ihre Gehirnsubstanz bei Wirbeltieren, mit Ausnahme des Menschen. Müllers Archiv für Anatomie und Physiologie, 320-345.

Hays, W.L. (1963) Statistics for psychologists. New York:, Holt, Rinehart and Winston.

Herrnstein, R.J. (1985). Riddles of natural categorization. Philosophical Transactions of the Royal Society, B, 308, 129-144.

Hilz, R.L., Huppman, G., and Cavonius, C.R. (1974).

Influence of luminance contrast on hue discrimination. Journal of the Optical Society of America, 64, 763-766.

Hodos, W. (1969) Color discrimination deficits after lesions of the nucleus rotundus in pigeons. Brain, Behavior and Evolution, 2, 185-200.

Hodos, W., & Bonbright, J.C. (1972). The detection of visual intensity differences in pigeons. Journal of the Experimental Analysis of Behavior, 18, 471-479.

Humphrey, N. (1971). Colour and brightness preferences in monkeys. Nature, 229, 615-617.

Jacobs, G.H. (1963). Spectral sensitivity and color vision of the squirrel monkey. Journal of Comparative and Physiological Psychology, 56, 616-621.

Jacobs, G.H. (1978). Spectral sensitivity and colour vision in the ground-dwelling sciurids: Results from golden-mantled ground squirrels and comparisons for five species. Animal Behaviour, 26, 409-421.

Jacobs, G.H. (1981). Comparative color vision. New York: Academic.

Jacobs, G.H. (1983). Within-species variations in visual capacity among squirrel monkeys (Saimiri sciureus): sensitivity differences. Vision Research, 23, 239-248.

Jacobs, G.H. (1984). Within-species variations in visual capacity among squirrel monkeys (Saimiri sciureus): color vision. Vision Research, 24, 1267-1277.

Jacobs, G.H., & Pulliam, K.A. (1973). Vision in the prairie dog: Spectral sensitivity and color vision. Journal of Comparative and Physiological Psychology, 84, 240-245.

Jitsumori, M. (1978). Wavelength discrimination function derived from post-discrimination gradients in the pigeon. Japanese Psychological Research, 20, 18-28.

Kalish, H.I. (1958). The relationship between discriminability and generalizastion: A reevaluation Journal of Experimental Psychology, 55, 637-644.

Kerr, L. (1974). Detection and identification of monochromatic stimuli under chromatic contrast.

Vision Research, 14, 1095-1105.

Kerr, L. (1976). Effect of chromatic contrast on stimulus brightness. Vision Research, 16, 463-468.

King-Smith, P.G. (1969). Absorption spectra and function of the colored oil drops in the pigeon retina. Vision Research, 9, 1391-1399.

Kirschfield, K. (1982). Carotenoid pigments: Their possible role in protecting against photooxidation in eyes and photoreceptor cells. Proceedings of the Royal Society of London B, 216, 71-85.

Konishi, T. (1965). Developmental studies on the retinal oil globules in Japanese quail (Coturnix coturnix japonica). Zoological Magazine, 74, (abstract).

Kovach, J.K. (1974). Early color preferences in the Coturnix quail. Journal of Comparative and Physiological Psychology, 87, 1049-1060.

Kovach, J.K., Wilson, G., & O'Connor, J. (1976). On the retinal mediation of genetic influences in color preferences of Japanese quail. Journal of Comparative and Physiological Psychology, 90,

1144-1151.

Levi, W.M. (1974). The pigeon (rev. ed.). Sumter S.C.: Levi.

Lombardi, C.M., Fachinelli, C.C., & Delius, J.D. (1984). Oddity of visual patterns conceptualized by pigeons. Animal Learning and Behavior, 12, 2-6.

Loop, M.S., & Bruce, L.L. (1978). Color vision: The effect of stimulus size. Science, 189, 1221-1222.

Lythgoe, J.N. (1971). The ecology of vision. Oxford: Clarendon.

Mariani, A.P., & Leure-DuPree, A.E. (1978). Photoreceptors and oil droplet colors in the red area of the pigeon retina. Journal of Comparative Neurology, 182, 821-837.

Martin, G.R., & Muntz, W.R.A. (1979). Retinal oil droplets and vision in the pigeon. In A.M. Granda and J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon (pp. 307-326). New York: Plenum.

Mayr, I. (1972). Vertellung, Lokalisation, und

Absorption der Zapfenölkugeln bei Vögeln (Ploceidae). Vision Research, 12, 1477-1484.

Mello, N.K. (1968). Color generalization in cat following discrimination training on achromatic intensity and on wavelength. Neurophychologica, 6, 341-354.

Mello, N.K., & Peterson, N.J. (1964). Behavioral evidence for color discrimination in the cat Journal of Neurophysiology, 27, 323-333.

Meyer, D.B., Stuckey, S.R., & Hudson, R.A. (1971). Oil droplet carotenoids of avian cones. I. Dietary exclusion: Models for biochemical and physiological studies. Comparative Biochemistry and Physiology, 40B, 61-70.

Milkman, N., Shapley, R., & Schick, G. (1978). A microcomputer based visual stimulator. Behavior Research Methods and Instrumentation, 10, 539-545.

Muntz, W.R.A. (1972). Inert absorbing and reflecting pigments. In H.J.A. Dartnall (Ed.). Handbook of sensory physiology: Vol. VII/1. Photochemistry of vision. Berlin: Springer.

Murton, R.K. (1965). The wood-pigeon. London: Collins.

Nelson, C.R., & Wasserman, E.A. (1981). Stimulus asymmetry in the pigeon's successive matching-to-sample performance. Bulletin of the Psychonomic Society, 18, 343-346.

Peeples, D.R., & Teller, D.Y. (1975). Color vision and brightness discrimination in two-month-old human infants. Science, 189, 1102-1103.

Peiponen, V.A. (1963). Experimentelle Untersuchungen über das Rotkehlchen, Erithacus rubecula (L), Annales Zooligi, Societas Zoologica-Botanica fennica Vanamo, 24, 1-49.

Romeskie, M., & Yager, D. (1976). Psychophysical studies of pigeon color vision - I. Photopic spectral sensitivity. Vision Research, 16, 501-503.

Schaller, M.J. (1975). Chromatic vision in human infants: Conditioned operant fixation to "hues" of varying intensity. Bulletin of the Psychonomic Society, 6, 39-42.

Schneider, B. (1972). Multidimensional scaling of color difference in the pigeon. Perception and Psychophysics, 12, 373-378.

Sidley, N.A., and Sperling, H.G. (1967). Photopic spectral sensitivity in the rhesus monkey. Journal of the Optical Society of America, 57, 816-817.

Sperling, H.G., Sidley, N.A., Dockens, W.S., & Jolliffe, C.L. (1968). Increment threshold spectral sensitivity of the rhesus monkey as a function of the spectral composition of the background field. Journal of the Optical Society of America, 58, 263-268.

Swets, J.A. (1964). Signal detection and recognition by human observers. New York: Wiley.

Wald, G. (1958). The Selig Hecht Commemorative lecture. National Physiological Laboratory Symposium No. 8, pp. 7-61.

Walls, G.L. (1942). The vertebrate eye and its adaptive radiation. New York: Hafner.

Wallman, J. (1979). Role of the retinal oil droplets in the color vision of Japanese quail. In A.M.

Granda & J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon (pp.327-352). New York: Plenum.

Werner, J.S. & Wooten, B.R. (1979). Human infant color vision and color perception. Infant Behavior and Development, 2, 241-274.

Wohlbarsht, M. (1976). The function of intraocular filters. Federation Proceedings, 35, 44-50.

Wortel, J.F., Wubbels, R.J., & Nuboer, J.F.W. (1984). Photopic spectral sensitivities of the red and the yellow field of the pigeon retina. Vision Research, 24, 1107-1113.

Wright, A.A. (1972). Psychometric and psychophysical hue discrimination functions for the pigeon. Vision Research, 12, 1447-1464.

Wright, A.A. (1976). Bezold-Brücke hue shift for the pigeon. Vision Research, 16, 765-774.

Wright, A.A. (1979), Color-vision psychophysics: A comparison of pigeon and human. In A.M. Granda & J.H. Maxwell (Eds.). Neural mechanisms of behavior in the pigeon. New York: Plenum.

Wright, A.A., & Cumming, W.W. (1971). Color-naming functions for the pigeon. Journal of the Experimental Analysis of Behavior, 15, 7-17.

Young, S.R., & Martin, G.R. (1984). Optics of retinal oil droplets: A model of light collection and polarization detection in the avian retina. Vision Research, 24, 129-137.