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Color Perception in Golden Mantled Ground Squirrels

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APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

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Squirrels appear to be unique among sub-primate mammals in being able to see at least some colors. A readily available Oregon squirrel species, golden mantled ground squirrels (<u>Citellus lateralis</u>), which has not previously been tested under laboratory conditions for color vision, was subjected to color discrimination testing in a Skinner box. On the basis of recent physiological tests of color reception capacity and behavioral tests of color discrimination response in closely related species, it was predicted that this species should be able to discriminate blue, green and possibly yellow, but not red. Three experiments were conducted. The first, a pilot study, checked for discrimination

of blue from green and blue from gray; subjects were rewarded for pressing on one color, shocked for pressing on the other color. The second experiment, the main part of the study, used one subject for each of three discriminations: green from gray, yellow from gray, and red from gray. Here, a choice approach was employed: two bars were used, with subjects having to choose the correct one for each stimulus, receiving a food reward for correct choices and no reward for incorrect choices. Third, a series of tests was devised to check for use of cues other than color as a possible basis for discrimination in the main experiment. These squirrels succeeded in discriminating all four colors, and results of the series of cue tests indicate they were not making significant use of non-color cues. Despite past results, therefore, it was concluded that this species is capable of seeing all colors in the visible spectrum. This result should be of interest to evolutionary theorists and may have important implications for current theories of color vision processes.

COLOR PERCEPTION IN GOLDEN MANTLED GROUND SQUIRRELS

by

ROBERT F. COOLEY

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TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

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John Wirtz, in the Portland State biology department, has worked extensively with golden mantled ground squirrels and retains a lively interest in them. It was a discussion with him which first alerted me to the interesting problem of this species' color vision capabilities, and he provided a working basis for this inquiry with his knowledge and bibliographical aid.

Gerry Murch was the source of such knowledge as I have gleaned of the problems in color vision theory and the implications for it presented by squirrels. He was also unstinting in providing technical knowledge and aid on brightness measurement and related problems, without which this experiment would have been impossible or extremely unsophisticated; and he kindly loaned equipment which was crucial to the experiment.

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And laboratory manager Ned Evers solved the seemingly insoluble problem of automating the reward feeding of sunflower seeds with a unique machine which probably should be patented, as well as spending a full week setting up and figuring out the automatic equipment for the second experiment.

My largely liberated lady provided neither coffee nor typing nor proof reading, so can't be thanked in the usual manner. She did, however, support me financially and psychologically through all this, and while it would doubtless have been possible without her I am indeed grateful.

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INTRODUCTION

For many years it was thought that, among the mammals, only primates possessed color vision. Recent investigations, however, indicate that some species of squirrels have retinas composed only of cones, which are normally color receptors; and physiological tests suggest that these retinal cones are sensitive to some colors at least (Tansley 1965; Michael 1966.) Since about 1960 the physiological work has been supplemented by a few behavioral studies of varying quality which support the thesis that the squirrel species studied can indeed see some colors.

C.R. Michael (1966, 1968b) measured responses of retinal ganglion cells to various wavelengths in the Mexican ground squirrel (Citellus mexicanus.) He found a blue-green opponent colors reaction; that is, some nerve fibers were excited by blue light and inhibited by green light, and some the reverse. Peak sensitivities were at 460 nm (blue) and 525 nm (green.) Michael reported finding no evidence of red-sensitive fibers or of a red-green opponent colors reaction.

Michael's results correspond in general to the spectral sensitivity curves established by other investigators for various species of squirrels; the general finding shows a maximum sensitivity around 525 nm and a secondary peak between 460 and 480 nm (in the blue range.) No evidence of a third peak in the red-orange area has been reported. (Cf. discussion of literature on spectral sensitivity in squirrels by Crescitelli and Pollack 1966; and

Figure 1, page 3, for an illustration of a spectral sensitivity curve[1].)

Turning to behavioral studies, the first serious laboratory effort reported was N. Bonaventure's work with the European ground squirrel (Citellus citellus) in 1959. He used a choice-box with different colored lights at each end and a food reward for correct choices. He reports that his four subjects discriminated between all of 13 pairs of colored lights used, covering the whole visible spectrum from 475 nm (blue) to 622 nm (red.) He used behavioral measures to establish spectral sensitivity and his results differ considerably from those others have reported (he found a single peak at 555 nm), so his brightness matching may have been off. Despite this, his work opens up the otherwise unexpected possibility of red perception in Citellus species.

Crescitelli and Pollack reported on a study using the antelope ground squirrel (Citellus leucurus) in 1966. They used a similar two-choice system, with the subjects going to one end or the other of a box and rewarded with food for correct choices. They used

[1]Spectral sensitivity curves are generally established by means of the electro-retinogram, which measures the electrical responses of a retina to light and establishes the retina's relative sensitivity to different wavelengths of light. ERGs based on the responses of cones indicate, then, the potential color perception abilities of a subject. Note that physiological spectral sensitivity does not by itself prove ability to see colors, since several species have adequate spectral sensitivity curves but appear to be behaviorally color blind or nearly so.

The spectral sensitivity curve also indicates which colors, given equal physical intensity of light stimuli, will appear brightest to a species. In humans, for example, the maximum peak in the spectral sensitivity curve occurs in the yellow area, and yellow appears brighter to us than other colors of equal physical intensity since our eyes are most sensitive to yellows.

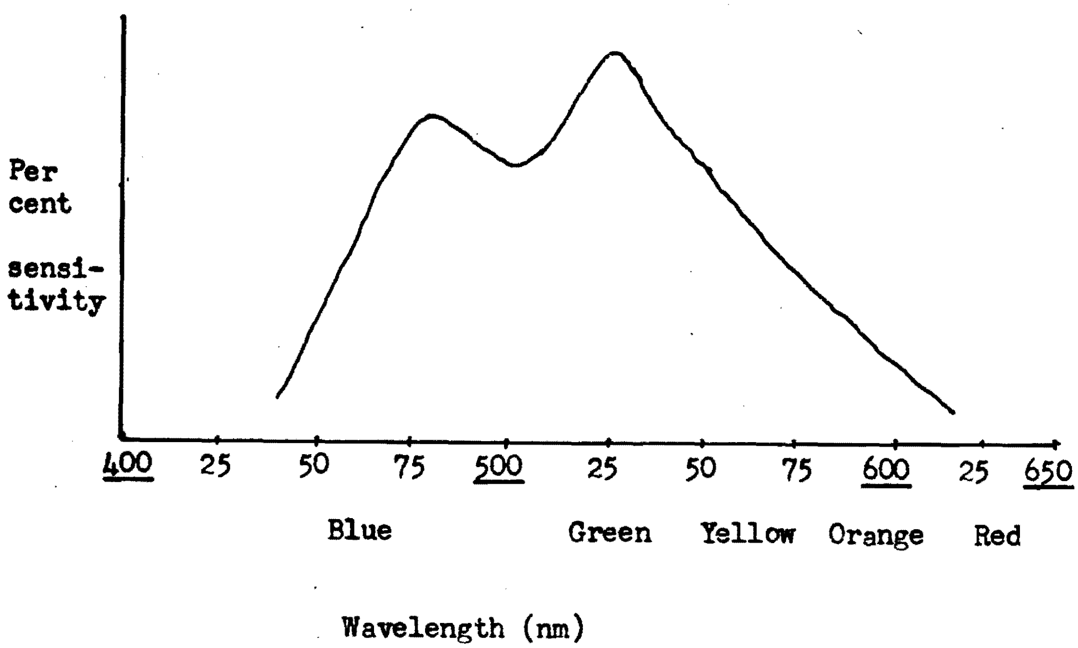

Figure 1. Spectral sensitivity curve for *Citellus leucurus* (approximate.) From Crescitelli and Pollack 1966.

four subjects, training each on one color and using several different colors as the incorrect or non-reward stimuli; thus, the blue-trained squirrel might be presented with blue vs. green, then blue vs. red, then blue vs. yellow, and so on. Their brightness control appears to have been adequate. They report good results for blue against other colors; partial success for green vs. other colors, but state that brightness could have been a factor in this case; slight but non-significant success with orange; and random performance with dark red (640 nm.) They did not use yellow as a positive stimulus color.

K.M. Michels and A.W. Schumacher tested two species of tree squirrels (Sciurus carolinensis and Sciurus niger) and reported in 1968 that all six of their subjects demonstrated good color discrimination ability in all areas of the spectrum, ranging from 465 to 620 nm. They also used a choice system, between pairs of colors and between colors and brightness matched grays. Brightness control may have been inadequate; they varied brightness randomly around matches equated for physical intensity rather than around matches equated on the basis of spectral sensitivity results, so that at some wavelengths their subjects would have perceived considerable luminance difference in physically matched pairs. However, the brightness variation used was great enough that this appears unlikely to be a possible basis for such consistent results.

The most thorough and careful work done to date was reported by G.H. Jacobs and R.L. Yolton in 1971. Many aspects of their subjects' color vision abilities were examined. In the behavioral color perception portion of their work, Jacobs and Yolton used three lighted ports on the same side of a box; below each port was a Skinner bar, which when pressed delivered a food reward for a correct choice. On each trial two of the ports had the same color, while the third was a different color; the subject was required to press the bar under the odd color to get his reward. (For example, if the colors were blue, blue and green, the squirrel had to press the bar under the odd, green port to get a reward.) Brightness was carefully controlled. Three subjects, two Mexican (Citellus mexicanus) and one thirteen-lined (Citellus tridecemlineatus) ground squirrels, demonstrated good discrimination ability at five wavelengths ranging from 452 nm (dark blue) to 538 nm (light green.) The investigators did not, however, test for discrimination on the longer wavelengths, yellow, orange, and red; presumably because they assumed failure on the basis of the physiological data.

(Please see Table I, page 6, for a summary of results of behavioral testing.)

The behavioral experimenters noted above used choice methods to determine discrimination ability: with two or more ports illuminated by one color each, the squirrels were rewarded if they moved toward or pressed a bar under the positive stimulus color, and received no reward if they chose the negative stimulus color. Brightness control was handled in various ways. Ground squirrels appear to be quite sensitive to brightness differences, and may use them in preference to color cues unless forced to depend on color alone (Bonaventure 1959; Crescitelli and Pollack 1966.) Controlling

TABLE I

RESULTS FROM PAST LABORATORY BEHAVIORAL INVESTIGATIONS OF SQUIRRELS

	blue	green	yellow	orange	red
Bonaventure, 1959 European ground squirrel	yes	yes	yes	yes	yes
Crescitelli & Pollack, 1966 antelope ground squirrel	yes	prob.	not tested	poss.	no
Michels & Schumacher, 1968 black and fox squirrels	yes	yes	yes	yes	yes
Jacobs & Yolton, 1971 Mexican & 13-line squirrels	yes	yes	not tested	not tested	not tested

for brightness is, therefore, vital; and it is difficult due to the spectral sensitivity curve, which, as indicated above, means that each species perceives some parts of the spectrum as being brighter than others when all parts are equal in terms of physical intensity. The basic approach was to equate brightness on the basis of spectral sensitivity curve tests, whether physiological or behavioral, and then to vary brightness of the stimuli enough to make up for any slight discrepancies in the initial match.

Results of the physiological and behavioral studies leave little doubt that ground squirrel species in the Citellus genus have the capacity to, and in fact do, see blues and greens. Their ability to see the longer wavelengths, from yellow to red, remains a more open and an interesting question; the physiological studies of spectral sensitivity indicate no retinal capacity for perception of the longer wavelengths. Bonaventure, however, reports good discrimination at all wavelengths, as do Michels and Schumacher, working with a different type of squirrel which, however, has the same spectral sensitivity set-up (blue and green peaks, no red peak) as do the citellids (Tansley 1965). Crescitelli and Pollack did not test for yellow but found their red-trained subject unable to discriminate red; Jacobs and Yolton did not bother to test yellow and red.

Current knowledge of color vision in squirrels, as summarized in these results, has two general implications. First, it bears on evolutionary theory, supporting functional as opposed to taxonomic theories. (Simplistically stated, taxonomic theories hold that higher abilities develop in higher members of a class such as the mammals;

functional theories maintain that abilities develop as needed anywhere within a class.) Since most squirrels and primates share diurnal, arboreal habitats, the existence of color vision in both may also provide some clues to its development when data on the specific abilities of many primate and squirrel species are assembled.

Second, the work on ground squirrels, if current results continue to be supported, suggests some difficulties with current color vision theory. According to the generally accepted trichromatic theory of color vision, a species or individual must be sensitive to at least two colors for discrimination between colors to be possible (cf. Hochberg 1964.) If it were sensitive to only one color, it would see only shades of that color and of gray; if sensitive to two colors, it would see those two colors and grays. To see all colors of the visible spectrum, sensitivity to three colors is necessary, and is sufficient because all colors can be created by a mixture of three basic ones -- a result which, it has been assumed, cannot be achieved by mixing just two colors. Trichromatic theory has, however, been unable to explain the situation with human protanopes: red-blind individuals who lack red receptors, having only blue and green sensitivity, but see yellows clearly. Since yellow is, according to trichromatic theory, a mixture of green and red, this should be impossible. This anomaly has been explained in various ways, but the neural mechanisms involved are not understood at present (Weintraub and Walker 1968.) Since squirrels seem to have a retinal set-up very similar to that of human protanopes and are easier to use for physiological experiments, they might be extremely helpful in examining and working out this problem with color vision theory if they are, like protanopes, able to see yellows. If they can also see reds their contribution might be even more important.

The present experiment was undertaken with both these implications in view: to add to the evolutionary picture by testing a new species in the laboratory (an earlier attempt, by Wirtz in 1968, to test this species for color vision in the field was inconclusive due to the difficulty of controlling brightness and other non-color cues adequately), and to add some data to color vision theory. The experimental hypothesis, based on past results with squirrels and on color vision theory, was that <u>Citellus</u> <u>lateralis</u> would be able to discriminate blue and green, would fail to discriminate red, and might or might no prove able to discriminate yellow.

Testing of this species was carried out in three stages. The first stage, described below as Experiment I, was largely unsuccessful and was relegated to the status of a pilot project. After the apparatus and procedure were redesigned as described in Experiment II, the major results on color vision ability were obtained. Experiment III was a series of short experiments designed to test for possible use of non-color cues by the subjects in their discriminations.

EXPERIMENT I

Subjects

Nine golden mantled ground squirrels were trapped in early September, 1972, in the Indian Ford/Metolius River area near Sisters, Oregon. Two escaped, one was released when it proved untameable. The remaining six were hand-gentled four days a week by hand feeding for four weeks, and then were pre-trained to bar press in a Skinner box for three weeks. Two of these animals were too timid to perform in this situation; four subjects remained for use in the experiments.

Apparatus

In the first experiment a standard Skinner box with a single lever, one porthole and a food cup, all on the same side of the box, was used. The porthole was round, one inch in diameter, and covered with a piece of frosted lucite. A single projector was aimed directly at the porthole, with its lens about 15 inches from it; a CZA-500 watt projector lamp was used. A Kollmorgan Color Systems neutral density wedge with a range from 0 to 1.0 was used to provide brightness variation; it was installed between the projector and the porthole. The colors were provided by Kodak Wratten gelatin filters: blue, No. 48, dominant wavelength 471 nm; green, No. 61, 536 nm; and neutral density (gray), No. 96. These filters do not yield a "pure" light of a single wavelength, but rather a limited band within a range of 60 or 70 nm (for the colored ones.) Their characteristics, are, however, precisely specified and they are adequate for this type of work. The Skinner box had a wired grid floor which was connected to a standard shock generator to provide the slight shocks used in this experiment. The photosensor used for brightness measurement was a PT 100 vacuum diode manufactured by International Light. Food rewards of sunflower seeds with their shells on were hand delivered through a small hole over the food cup.

Procedure

After pre-training for bar pressing, each squirrel was trained on a pair of colors, blue and green, which were shown one at a time in random order in the single porthole for a 40-second interval. If the subject pressed when the positive color was showing, he received a sunflower seed reward; if he pressed when the negative color was showing, a button on the shock generator was pressed manually to deliver shock through the grid floor. The shock used varied from .08 to .5 milliamperes and from .075 to 1.0 seconds in duration. Two subjects were trained with blue as the positive color and green negative, and two with green positive and blue negative; each ran about 60 trials per day. Brightnesses were not matched until the fifth day of training; thereafter they were matched on the basis of the human spectral sensitivity curve, which approximates that of the ground squirrels (cf. Appendix A for discussion of brightness matching.) In the case of the two subjects whose performance appeared to be better than chance, brightness variation was also introduced, using the neutral density wedge. This is a shaded glass wheel which shades off from dark (density 1.0) to clear glass (density 0.) Three settings, dark, medium, and clear, were used with each color in random order. Subjects were scored correct if they bar pressed one or more times when the positive color was on, incorrect if they failed to press when it was on; correct if they did not press at all when the negative color was on, incorrect if they pressed one or more times when it was on.

Results

One squirrel, Roi, trained to blue as the positive color and green as negative, showed good discrimination after only six days of testing. After several more days of training, he performed at a 93 per cent level in one session, getting 56 out of 60 trials; he made one error on blue (failing to press at all during that interval) and three on green (pressed on three green intervals.) Roi was then shifted to blue vs. gray, with blue remaining the positive stimulus. After just 10 training trials on his first day, he produced a record of one error, on gray, in 60 trials for a score of 98 per cent; the following day he made four errors on gray, none on blue, in 60 trials for a score of 93 per cent. He was then shifted to green vs. gray, with green negative and gray positive. After nine days of training on this problem, his best performance was 29 correct in 47 trials, or 62 per cent, on an incompleted schedule; this is not significant at the .05 level using a one-tailed test for differences between proportions. With this subject a shock of .08 milliamperes for .075 seconds was employed throughout.

The other three squirrels were much less successful. Stumpy, trained on green positive, blue negative, produced after 16 days a record of 31/45, or 69 per cent (17/28 on green, 14/21 on blue), which does indicate discrimination (significant at the .05 level, one-tailed.) That schedule was not completed, however, and his performance deteriorated after that. The other squirrels failed to perform at levels much above chance. With these three squirrels differing shock intensities and durations were used, in the ranges indicated.

Discussion

This approach to discrimination testing — using a single lighted port and bar, and shock for incorrect presses — was selected partly because it seemed easier to set up on a manual, non-automated basis than the choice approaches used by other experimenters; and partly because past results indicated that squirrel subjects generally performed at best around the 70 per cent level in discriminating in a choice situation. As the literature on shock in connection with simple discrimination learning in rats suggests that at low levels it improves performance, it was thought that speed of training and level of final performance might be improved by using shock in this situation with squirrels. To the contrary, however, this method proved quite inefficient; and when, after 21 days of training, the one squirrel who was doing fairly well with this method, Roi, died over Christmas vacation, the shock approach was abandoned. Retrospectively, however, it is not clear whether the problem with this procedure was the shock or the lack of uniformity in timing of reward delivery and so on created by the manual operation (cf. Appendix II for brief discussion on use of shock.)

The results did indicate that this species can discriminate blue from green and blue from gray, so the ability to see blue was established. Whether green was also seen as such, or appeared as a gray which could be distinguished from blue by the squirrels, was an open question; and yellow and red had not been dealt with at all.

EXPERIMENT II

Subjects

The three surviving subjects of Experiment I were used again, following a break of six weeks while new equipment was set up and a two week period of pre-training in the new Skinner box and situation.

Apparatus

The new set-up was completely automated except for counting, and employed a two bar choice approach rather than the response vs. no response method used in Experiment I. Due to equipment limitations, however, it was only possible to use a single porthole, with one color showing at a time, rather than having one port and one lever for each color.

The new Skinner box had one lever on each side of one of its faces, with the light porthole between the two levers and the food cup located directly below the porthole. The porthole was rectangular, measuring 1 1/8 inches long by 13/16 inches high, and was again covered with frosted lucite. An automatic feeder mechanism for sunflower seeds was devised and located directly in front of the porthole and food cup. Two projectors were used, located on either side of the automatic feeder and aimed at the porthole. The projector lenses were approximately 6.5 inches from the porthole, at about a 30 degree angle to it. One projector used a CZA-500 watt bulb, the other a DEK-500 watt. Each contained a single slide. Other equipment was as before, with the addition of Kodak Wratten filters No. 9, yellow, 581 nm, and No. 25, red, 620 nm. A random tape, randomized over 40 trials but with no sequences of more than three presentations of a single color in a row, controlled the sequence of color presentation. In an effort to eliminate possible non-color cues from stray light or view of the experimenter the Skinner box was placed inside a cardboard box with holes cut in the front for the feeder tube and the two projector beams, and a large hole cut in the top for outside light. (Being strictly diurnal, ground squirrels tend to go to sleep when it's dark.) Since the overhead room lights were very bright and the subjects seemed unable to tell the darker grays from a "lights off" condition (due to the amount of light coming through the porthole from the room illumination), a desk lamp was placed directly over the box and the overhead lights were turned off while subjects were performing, so that when the projectors weren't on the porthole appeared quite dark. (Please see Figure 2, page 17, for a diagram of the apparatus set-up.)

Procedure

The operation was as follows: One of the two projectors comes on; if it is, say, yellow, the squirrel must press the right-hand bar to get a sunflower seed. This projector stays on for 22 seconds, and the squirrel is rewarded for each press of the correct bar during that interval; normally he gets in two or three presses. Then follows a nine-second "lights out" interval, during which presses are not rewarded, and then a projector comes on again. If it is the other projector, which in this case would be gray, the squirrel must now

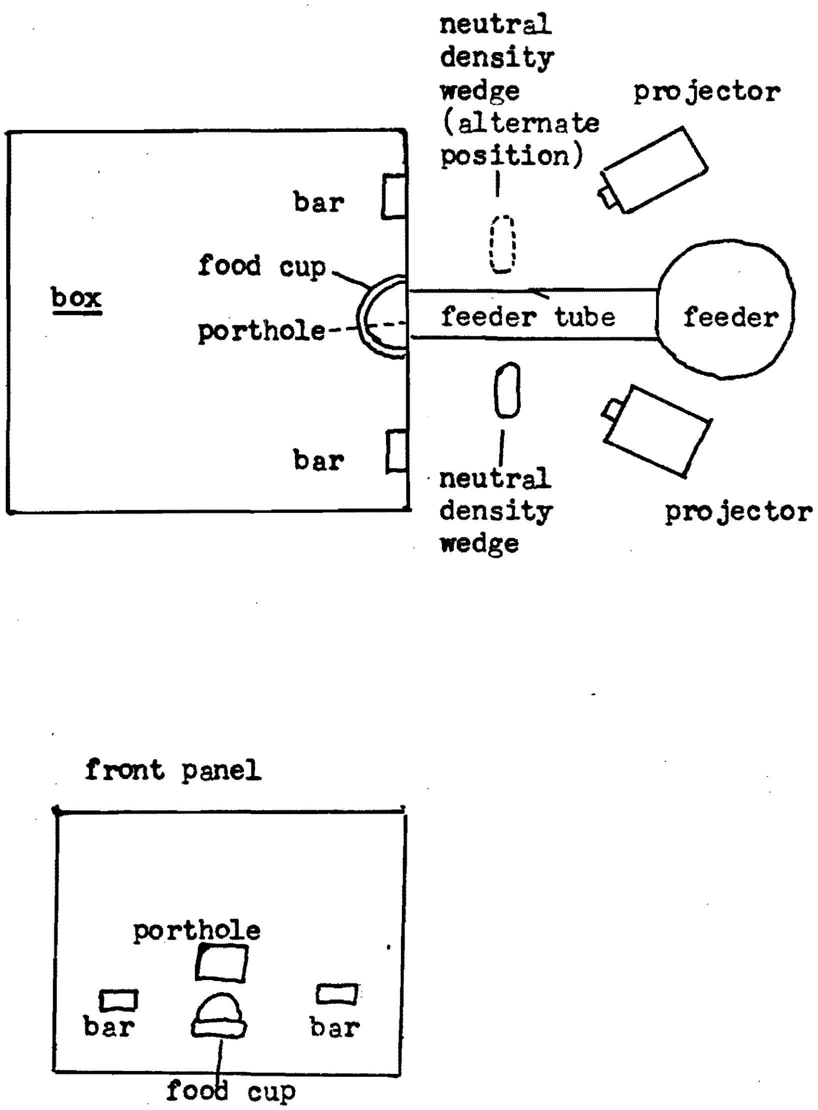

Figure 2. Top and inside views of apparatus for Experiment II.

press the left-hand bar to get a reward. If the squirrel presses the wrong bar when the porthole is illuminated, there is no reward and the projector shuts off and remains off for the duration of its 22-second "on" interval. During this time any presses are unrewarded. Scoring was by intervals rather than by presses. For any one "light on" interval, the squirrel was scored as correct if he made one or more correct presses and no errors; as incorrect if he pressed the wrong bar at any time during the interval, even after a correct press, as sometimes happened; and was not scored at all if, as also occasionally occurred, he declined to press at all during the interval.

Approximate brightness matching was again achieved by using neutral density filters (gray) of varying darkness so that the two slides used for each squirrel were of approximately equal luminance. The neutral density wedge was used in the same way as in the first experiment: at a dark setting, a medium setting, or not used at all to give a bright condition. The order of these conditions was randomized through the 40-trial tape; in 40 trials, each slide appeared six times at a dark setting, six times at a medium setting, and eight times at bright. Since it appeared early in the training period that the squirrels were discriminating well on yellow and red, which was not expected, extra variation was introduced to cut down the possibility of discrimination on the basis of brightness. The 40-trial sequence was divided into two halves, each 20 trials long, and a Log 1.0 filter was used with the colored slide (e.g. green) so that it appeared quite dark relative to the gray slide; then it was shifted to the gray slide, so that the gray slide now appeared quite dark for 20 trials; then it was removed altogether, so that both slides, colored and gray, appeared approximately equally bright for 20 trials. Thus, in 60 trials, each condition -- color dark, gray dark, and matched -- occurred 20 times. The neutral density wedge was still being used, and since it has a maximum density of 1.0 also, the effective variation, combining both the wheel and the extra 1.0 neutral density filter, was 2.0. Since Log 2.0 transmits only one per cent of the available light, the variation in terms of total percentages ran from 100 per cent to one per cent. Each slide appeared, randomly, at six different brightnesses throughout 60 trials.

This is as much variation as has been used by other experimenters working with squirrels, and, with the 500-watt projectors, approached the limits of what the squirrels could handle: at 2.0 they apparently had difficulty in seeing the illumination. Indeed, in the case of the red slide, which was much darker than the green and yellow, the extra filter had to be limited to 0.7 instead of 1.0, since the squirrel either performed at random or refused to press under the 2.0 situation. Log 1.7 (1.0 on the wheel plus 0.7 slide) transmits only two per cent, so this variation should not have affected the results.

As it appeared from the first experiment that these squirrels would not transfer particularly readily to new problems, the design used here was very simple: to test each of the major remaining colors -- green, yellow and red -- against a brightness matched gray. Since three subjects were available, each was trained on one of the colors.

After pre-training in the new box, the discrimination problem was introduced in early March, with brightnesses only roughly matched. All squirrels were apparently discriminating to some extent after five days (over 60 per cent correct.) When final brightness matches were introduced two days later, it appeared that the new relative brightnesses involved caused considerable difficulty in two cases (yellow and red.) However, by the end of the second week all three subjects were again discriminating adequately (at least 70 per cent this time.) Early in the third week the brightness problem was explored -- the additional Log 1.0 gray filters were introduced at this time -- and at first two of the squirrels (green and red this time) again did poorly with radical brightness changes; but they soon learned how to handle them -- presumably, by becoming less dependent on brightness as a cue. At the end of the third week final testing was begun, with 240 trials, spread over from two to four days, run with each subject.

Results

Results for the final 240 test trials were: Stoney, green vs. gray, 77 per cent (182/237). Took two days to complete. Did less well when the gray filter was dark (with the extra 1.0 filter added to it), getting 52/77 under that condition (68 per cent) vs. 64/80 (80 per cent) when green was dark and 66/80 (83 per cent) when both were bright (and approximately matched.)

Mack, yellow vs. gray, 85 per cent (202/237.) Required three days for completion. Did slightly better under matched conditions (72/80) than with yellow dark (65/80) and gray dark (65/77.)

Stumpy, red vs. gray, 83 per cent (198/237.) Four days for completion. On red dark, 62/80; on gray dark, 66/77; on matched, 70/80.

(Please see Figure 3, page 22, for a graphic summary of these results.)

The differences between performances under the different conditions were non-significant except for Stoney (gray vs. green); the difference between his performance under the gray dark condition and the other two conditions was significant at the .05 level using a one-tailed test for the difference between proportions. Overall the subjects did somewhat better under matched conditions (87 per cent) than under the other two (80 per cent for color dark, 79 per cent for gray dark), though the difference is non-significant.

Discussion

These results are simple and clear-cut: unless brightness or other cues were being used by the subjects, this species is able to see all the colors of the visible spectrum.

With the use of the Log 1.0 filter alternating between the two slides, it was thought that if any of the subjects were using brightness rather than color cues, they would show a reversal performance under one of the three conditions. For example, if when luminance was supposedly matched between green and gray the gray actually appeared brighter than the green, then, if the subject were using brightness as a basis for discrimination, he would also do well when the green slide was darkened by the extra 1.0 gray filter, but should show a reversal performance under the gray dark condition. Though the gray vs. green

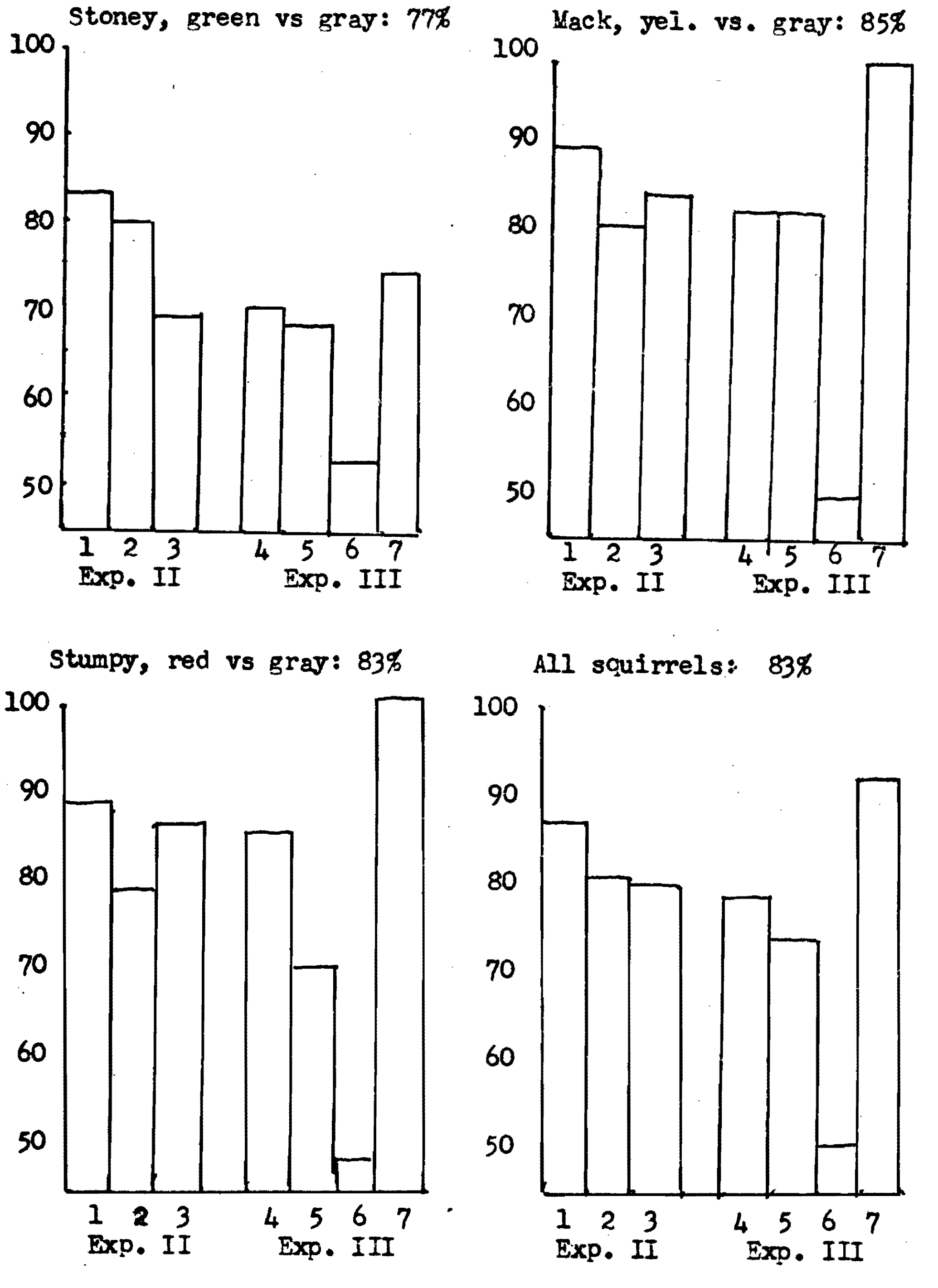

Figure 3. Results summarized: per cent correct choices by conditions, Experiments II and III. Interval key: 1, matched brightness; 2, color dark; 3, gray dark; 4, projector reverse; 5, brightness test; 6, blue vs. blue; 7, color reversal, per cent incorrect.

subject shows a tendency in this direction, his 68 per cent correct when gray was dark is still significantly different from a random 50 per cent, so this is not even a random performance, let alone a reversal performance. Brightness may have been used as an adjunct to his discrimination, but it apparently was not a primary cue. The overall performance of the three subjects, though not significant in the differences between conditions, shows an unlikely trend if brightness were being used, as one would expect in that case that they would do much better under one of the "dark" conditions, rather than under the "matched" condition. The difference may be due to the greater difficulty of seeing the darker slides.

EXPERIMENT III

The above results were surprising in light of the experimental hypothesis, based on past results and color vision theory, and led to an additional series of short experiments designed to check for possible non-color cues that the squirrel subjects might be using as a basis for their successful discrimination. There were several possible sources of such cues. Brightness was the most obvious one; concern about that led to the greater variation in brightness employed in the second experiment, and to one of the check experiments. Sound cues were a possibility, since the automatic set-up relay switches emitted at least one small click which a color blind but alert human subject could have used as a basis for successful discrimination, and it was also possible that the two projectors sounded slightly different when projecting than when only their fans were operating. The most serious problem was that, due to mechanical considerations, it was not deemed feasible to design the set-up so that the two stimulus slides could be moved from one side to the other; the gray slide was always projected from the right hand side facing the box, and the colored slide from the left hand side. This might have produced cues based on both light angle and stray light, despite the attempt to eliminate such cues by enclosing the Skinner box in a cardboard box. These short experiments, and their results, were as follows (cf. Figure 3, page 22, for graphic summary):

Short Experiment A

Procedure. First, for 40 trials, a different random tape was used (in case the subjects had learned the order of the standard one); most importantly, the projectors were reversed so that the slides were now projected from opposite sides (colored slides from the left, grays from the right); the projectors were moved further back, which reduced the absolute brightness of the slides while maintaining relative brightness (in case the subjects had learned to pick out specific absolute brightnesses), and different settings were used on the neutral density wedge (for the same reason.)

Results. The green-gray subject dropped from his test average of 77 per cent to 70 per cent on this test; the other two subjects continued very close to their main study averages, getting 83 and 85 per cent.

Short Experiment B

Procedure. For 40 trials, with the projectors still reversed and further away, maximum brightness variations were used. Since in Experiment II the Log 1.0 filter was moved every 20 trials only (from one slide to the other), it seemed possible that if the subjects were really good at brightness discrimination they might miss just one or two trials after each shift and then adjust to the new brightness levels; performance records suggested that this was possible. So, for these 40 trials, the 1.0 gray filter was moved every four trials, and the darkest neutral density wedge setting was used with whichever slide was dark. The subject was thus faced with two bright yellow trials, say, versus two grays with additional Log 2.0 interference (presented randomly, of course); and then the reverse, two bright grays vs. two yellows with Log 2.0 interference.

<u>Results</u>. Results here were 82 per cent for the yellow-gray subject; 68 per cent for the green-gray (compared with his main study average of 77 per cent); and 71 per cent for the red-gray subject (compared with a main study average of 83 per cent.) Sixty trials were done with this last subject, instead of 40, as he did very poorly on his first 20 trials (60 per cent.) Over the last 40 trials he got 75 per cent, and 80 per cent over the last 20.

<u>Short Experiment C</u>

<u>Procedure</u>. The slides were reversed. Whereas before the squirrel had to press the right hand bar with a colored slide, the left hand bar with a gray slide, now, in order to get a reward, he would have to press the left bar with the colored slide, the right bar with the gray slide. If he had been discriminating primarily on the basis of color cues, he should fail at this task: when a color is presented, he would continue to press the right-hand bar, which now will <u>not</u> reward him, and when gray is presented, he would continue to press the left-hand bar, which likewise will not reward him. If, on the other hand, a subject had been discriminating on the basis of projector light angle, shadows cast differently by the two projectors, or projector sound, this task should present no problems; being conditioned to press the right-hand bar when the right-hand projector is on, he will continue to do so, and will

continue to be rewarded, even though the color stimulus is now gray instead of colored. Two squirrels were given two 10-trial tests (five color intervals, five gray intervals) at this task at different times; a third was tested for 20 trials on a single occasion.

Results. On the four 10-trial tests, 100 per cent of the trials were missed; on the 20-trials one, 75 per cent were missed (seven of the first 10 and eight of the second 10 trials.)

Short Experiment D

Procedure. Fourth, and finally, two blue filters were used, one in each projector; if cues other than color and brightness were being used, the subjects should have been able to discriminate between the two slides.

Results. The results were 21/40, 20/40, and 19/40 correct.

Discussion of Short Experiments

The first two cue tests indicated some difficulty, particularly with Stoney, the gray-green subject, who performed at somewhat below his main study average on both tests. This could indicate that, on the first test, projector angle cues played a part; and, on the second, that either projector angle cues (since the projectors were still reversed) or brightness cues played a part, in his previous successful discrimination. However, if projector angle cues were the major basis of his discrimination, these tests would have led to a reversal performance (approximately 25 per cent correct) rather than just to lowering his success; and if brightness were a major factor, his success on the second test would have been limited to a random performance (50 per cent correct) and would probably have been worse than that. Since far from reversing or falling to random performance he continued to discriminate at a significant level, it appears doubtful that those cues were primary ones for him. It certainly remains possible that projector angle and/or brightness differences were used as secondary cues. An equally plausible interpretation of his difficulties in the second test, for brightness, would be that he had difficulty seeing the extremely dark colors.

This interpretation also appears applicable to Sumpy's performance on the second test. His performance was poor on the first 20 trials due to the fact that he refused to press the left bar at all, a response pattern which seemed to indicate confusion. (This squirrel had the same reaction early in training when the relative brightnesses of the test stimuli were reversed inadvertently; and all three subjects reacted in the same way when confronted with the two blue filters in the fourth cue test.) Since his performance level improved to an adequate rate over the last 40 trials and the question on this test is purely one of maximum performance, his initial drop-off does not represent a serious problem in terms of use of brightness as a cue.

The third cue test was designed to check two things. First, if cues other than color and brightness were important, such as light angle, sound, etc., the subjects should have done fairly well, if not as well as usual, despite the slide reversal since they would still have other cues to go on. This proved not to be the case. Second, it seemed worthwhile to find out what happened under reversal conditions. During testing in the main study it was often the case that, after the Log 1.0 filter was shifted, a subject would miss two or three of the first five trials. The brightness change was clearly affecting performance, but was the subject using brightness as a primary cue? If so, the shift of the 1.0 gray filter would create a reversal situation. If these squirrels' normal response to a reversal were a random performance, it could well be that they were using brightness as the primary cue and reacting with a random performance for a few trials when brightness was reversed, before catching on to the reversal and altering their performance appropriately. This also proved not to be the case; since the squirrels' reaction to a reversal, as demonstrated in this cue test, was a complete performance reversal, it seems unlikely that that was what was taking place when the Log 1.0 filter was shifted during the main study.

The final cue test was an additional check on projector angle cues and a particular check on sound cues. Had either sound or projector angle been used as a major discrimination cue, the subjects should have performed at better than chance on those trials.

Although the experimental set-up left open the possibility that non-color cues were present and could have been used, this series of tests appears to eliminate the possibility of their use. The tests do indicate that brightness may have been used to some extent as a secondary but minor cue, or at least that sudden brightness changes could cause some confusion; this is apparent, too, from examining performance results from the main study.

CONCLUSION

It is clear from field studies that ground squirrels are adept at using many cues, such as smell and position, to get to a food source (Wirtz 1967; Gordon 1943); and from laboratory work it is obvious that they readily make use of brightness cues, perhaps preferring them to color cues as a basis for discrimination when both cues are available (Bonaventure 1959; Jacobs and Yolton 1971.) Thus, although a careful effort was made in this experiment to eliminate non-color cues, and the possible use of such cues was checked by additional tests with negative results, it is not impossible that the experiment was flawed and its finding, that *Citellus lateralis* has complete color vision, is inaccurate. That seems unlikely, however.

This leads to the question of why two other investigations on color vision in ground squirrels have not shown the same result. The most obvious possibility is that the different species investigated have different capacities. Other possibilities remain open, however.

The work by Crescitelli and Pollack, though physiologically sophisticated and extensive in behavioral investigation, had several shortcomings as they report it. First, their light source was automobile light bulbs on a six-volt system; it appears quite possible, from the performance of the subjects in the present experiment, that this would not provide sufficient intensity for discrimination in some cases. Second, in their main procedure the experimenters used a system where the two colored lights were at opposite ends of a long box; the stimuli were thus widely separated, and could not be compared to each other by the subjects in a single glance. Third, following the pressing of a bar under the port, the subject had to return to a central feeding station to get a reward or to learn via non-reward that he had pressed the wrong bar; this latency could make training more difficult. Fourth, it appears that several procedures were used with each subject (though this is not entirely clear from the published report), and that the procedure was not automated; from my own experience, it seems clear that the use of a single procedure, well automated so that the conditions remain very constant, may be important to successful discrimination training with squirrels. The Crescitelli and Pollack results almost exactly parallel the results of my first experiment, as well as showing many of the same procedural problems: good success on blue, partial success on green -- and then, less success yet on orange and red, which I did not test in my first experiment. This suggests that ground squirrels easily see blues, and have fair success with green, while having difficulty with orange and red; but it certainly does not prove, given their "n" of one each on orange and red, that Crescitelli and Pollack's antelope ground squirrels are unable to discriminate orange and red. Yellow, unfortunately, was not tested.

The failure of Jacobs and Yolton to show discrimination of the longer wavelengths is simpler and more disturbing: they failed to test them. On the basis of the physiological data on spectral sensitivity, and extrapolation from the results they did secure, they concluded that "it seems unlikely that either the 13-line or Mexican ground squirrels would be successful at discriminating" in the range from 575 nm to 622 nm; and they left it at that. The longest wavelength they examined carefully was 538 nm, green; they indicate that one subject successfully discriminated 560 nm from gray, but fail to say why they didn't pursue this success (Jacobs and Yolton 1971.) One is forced to conclude that theory interfered with science in this case.

The behavioral work done to date on squirrel color vision is obviously scanty as well as mixed in its conclusions; it is to be hoped that continued experimentation, both with new and with already examined species, will clear up this field, laying the groundwork for further work and theory.

As suggested in the introduction, the implications of this work, once it is on a firm footing, should be interesting in at least two different fields; evolutionary theory and color vision theory. In the long process of my experimentation and related research, I have acquired some interest in both these directions and can't refrain from summarizing the possibilities as I understand them; but I hasten to say that I am no expert in either biology or the intricacies of color vision theory, and to apologize for the inevitable shortcomings in the following suggestions.

In terms of evolutionary theory, there is no obvious reason based on present squirrel environments for the development of color perception. The various species are not brightly colored nor sexually differentiated in terms of color markings, as are many of the birds and reptiles which have color vision; and their food sources and general environment are not particularly colorful either. Indeed, it appears from Wirtz's field study of color perception with golden mantled ground squirrels, and from Bonaventure's laboratory experience with the European ground squirrel, that color perception ability is little used in the natural environment. It would be possible, as suggested by Dr. Murch (personal communication), that the all-cone retina developed as an adaptation to arboreal life (since largely abandoned by the ground squirrels), since squirrels do not have binocular vision and the much smaller size of cones, relative to rods, would give squirrels greater visual acuity which would be useful in animals using only motion parallax and other non-binocular depth cues to accurately judge leaping distances from branch to branch. However, if that was the basis for the development of the all-cone retina, it is hard to see why neurological processing of color as such should also develop. The problem is likely related to the habitat in some way, however, since primates and diurnal birds also have color vision (so do many reptiles, however, in a habitat more like that of ground mammals) and share with the squirrels a three-dimensional, daylight life. Perhaps, when more species of squirrels and other animals have been tested for color vision, someone will be able to fit the pieces together to arrive at a theoretical understanding of the development of color vision.

The possibility of full spectrum color vision in squirrels is also interesting in terms of physiological color vision theory. The physiological evidence for the existence of blue and green sensitivity, but no red or yellow sensitivity, in the retinal and adjacent ganglion cells of squirrels appears quite solid. If it is true that squirrels see reds and yellows as well as blues and greens, the squirrel species offer an excellent opportunity for laboratory investigations of the physiology of their color perception which would shed new light on the nature of color vision.

Based on present knowledge, the most likely explanation for the squirrel situation is some type of opponent color processing at a higher neurological level than the retina and its ganglion cells. Yellow perception in the case of human protanopes has been explained on such a basis: in addition to trichromatic perception at the retinal level and color mixing of the three basic colors to create the various hues, there may be at a higher neurological level yellow coded cells which are inhibited in the presence of blue light but stimulated when non-blue light is present (cf. Hochberg 1964.) A similar process could explain red and yellow perception in squirrels: cells which are inhibited in the presence of blue and green light, but are stimulated into firing when light other than blue and green is present. Land has demonstrated that it is possible, using only red and green light, to create the perception of the full spectrum in humans (Weintraub and Walker 1968). Thus retinal sensitivity to only two colors does not rule out the possibility of perception of the full spectrum; but if such is the case with squirrels, our present understanding of the mechanisms involved is poor. Fortunately, squirrels make good laboratory subjects, and may provide the means to improve our color vision theories.

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APPENDIX A

BRIGHTNESS CONTROL

Brightnesses were matched for the human eye, using the available data on the human spectral sensitivity curve which is not too different from those of the citellids. It was felt that this would give settings more closely matched for the squirrels' eyes than would a physical intensity matching. Matching on the basis of the curve for this species would have involved complex physiological testing, a major project in itself, and was considered unnecessary. No attempt was made to match brightnesses exactly; the assumption was that if they were fairly close, the random variation in brightness provided by the neutral density wedge and the additional gray filters would make a straight brightness discrimination impossible.

Correction factors were derived for each filter used by multiplying the correction factors for the human spectral sensitivity curve, corrected for P_{3000} projector lamps (Wyszecki and Stiles 1967, p. 300) times the correction factors for the photosensor used (Murch 1972) times the transmittance figures for the Kodak Wratten filters used (as published by Kodak.) In each case, the figures were calculated at 10 nm intervals from 400 to 650 nm (except for the neutral density filters, where only the range from 480 to 600 nm was used) and summed for each filter. For the neutral density filters, calculations were based on the Log 1.0 data published by Kodak and adjusted according to transmittance for other densities; e.g., 1.1 transmits 79.5 per cent as much as 1.0, and the correction factor for 1.1 was arrived at by taking 79.5 per cent of the 1.0 correction factor. This introduces some error since the Wratten neutral density filters transmit slightly less light than a theoretical perfect filter (about 91.7 per cent as much at 1.0), but the error was not great enough to be worrisome as there was no attempt to match luminance exactly.

TABLE II

FILTER CORRECTION FACTORS

Blue	80.5969
Green	1,388.0463
Yellow	6,286.1675
Red	685.5969
Log 1.0	727.5530
Log 0.2	4,583.5826
Log 0.9	923.9921
Log 1.1	458.3583

TABLE III

MEASUREMENTS USED IN CALCULATING BRIGHTNESS MATCHES

	Reading	Corrected Reading[1]
Experiment I		
Blue	141	141
Green plus 0.7	46	158
1.5	42	120
Experiment II		
Green	108	same
0.9	126	84
Yellow	370	same
0.2	620	453
Red	33	same
1.2	57	38

[1]The corrected reading is obtained by using the ratios of correction factors. For example, the ratio of the 0.9 correction factor to the green factor is .67. This ratio is multiplied by the actual neutral density filter reading to get the corrected, "true luminance" (for the human eye) reading for the gray filter. In this case, as can be seen, the "match" had a slightly darker gray than green as the human eye would see it.

TABLE IV

TEST DAY BRIGHTNESS READINGS

	Bright	Medium	Dark
Experiment I			
Blue	120	50	22.2
Green plus 0.7	39	16.2	7.2
Blue	107	45.9	16.8
1.5	42	18	6.6
Green plus 0.7	42	17.4	7.6
1.5	41	17.4	7.5
Experiment II			
Yellow	370	147	39
Yellow plus 1.0	36	15	3.8
0.2	620	255	66
1.2	52	21	5.4
Red	33	12.3	3.4
Red plus 0.7	6.4	2.5	.66
1.2	46	19.2	4.9
1.9	12.6	5.1	1.26
Green	108	41	10.8
Green plus 1.0	9.3	3.7	.93
0.9	126	51	13.2
1.9	12.6	5.1	1.26

APPENDIX B

LABORATORY BEHAVIOR

Golden mantled ground squirrels proved to be good laboratory subjects, despite some problems; since their laboratory use may become more frequent, it seems worthwhile to append some notes on my procedures and problems.

These animals were more difficult to handle and more susceptible to being upset than are laboratory rats. About half the potential subjects proved impossible to use because they were either too wild to handle at all or too timid to perform. A good deal of time was wasted trying to salvage some of these animals as subjects, which would have been better spent in trapping twice as many to begin with and planning to let difficult individuals go after two or three weeks of gentling and pre-training had separated the good subjects from the bad.

The better subjects were easily conditioned, after 10 to 15 days, to sit on one's hand to eat sunflower seeds. This effort seems worthwhile, since the subjects so trained were later easier to move about and less frightened of the experimenter and the experimental situation than were two squirrels who were good subjects but were not hand gentled. Over a period of two years of working with these animals at home and in the laboratory, I have never been able to gentle them to the point of being held in a closed hand without biting fiercely, or to accepting being moved around on an open hand without jumping off. Some system of moving subjects from their cages to the experimental apparatus in small containers has to be devised therefore; and gloves are required equipment for moving them by hand.

In new situations even well gentled squirrels are frightened; first placed in a Skinner box, they will adopt a "freeze" position and maintain it for two or three hours in most cases, and up to 20 hours in the case of a timid subject, even when they are quite hungry and food is available in the box. Pre-training, therefore, requires considerably more time and patience than in the case of rats.

Due partly to this timidity, great regularity in the experimental use of these animals pays off. During the first experiment, in the fall, the experimental set-up was almost entirely manual, making for irregularities in timing; and, with the exception of one squirrel which began discriminating quickly, shock levels were varied to try to improve performance. Additionally, the subjects were run just four days a week and at different times during the day. In the second experiment, the set-up was fully automated and therefore very regular and consistent, and subjects were run six days a week at the same time each day. While part of the success of the second experiment may be attributed to its being done in the spring, when the subjects were more active and hungrier, and to not using shock, my impression is that the regularity of the set-up was the main reason for greater success.

The use of shock may be worth exploring further; the one subject who did learn to discriminate during Experiment I learned no more quickly than the three subjects of Experiment II, but did achieve a much higher percentage of correct responses, 93 and 98 per cent, than was obtained under the non-shock Experiment II (77, 83 and 85 per cent.) At the lower levels of shock used, down to .08 milliamperes for .075 seconds, the shock produced no visible effect such as startle or paw licking. At .5 milliamperes, the maximum shock used, startle was occasionally apparent; and at 1.0 seconds duration, the longest employed, foot moving and paw licking occurred. Maximum intensity and duration were never employed together. In retrospect it appears that, despite the lack of visible reaction, the minimal shock level and duration were sufficient to the purpose and produced the best result. The other three animals tended to press many times in a row despite the shocks being received, and all eventually developed frustration behaviors: trying to get out of the box, grooming, sleeping. Whether this frustration was due to the shock or to inability to master the problem and get consistent rewards is difficult to say.

Some food deprivation was used but not a great deal; since weights were not recorded due to the difficulties involved, this is a subjective evaluation. During the winter experiment, when the subjects were getting about 100 seeds during a training session, they were fed approximately 20 additional seeds and one whole rat biscuit after the session. In the spring, they were averaging about 200 seeds per training session, getting fed 10 to 15 seeds and one half rat biscuit after the session, and with rare exceptions were still eager to perform the next day. Due to their spring voracity experimental sessions could be quite long. Whereas other experimenters have apparently used a maximum in the area of 50 trials per day, these three subjects endured from 60 to over 120 trials. Differences were due to the number of presses per interval rather than to appetite: one subject consistently pressed five or six times per interval, another only one or two times. All were ready to quit after approximately 200 seeds.

The main diet was sunflower seeds, by far the preferred food, with rat biscuit for balance. The rat biscuit was at first refused, but after one or two months all subjects were willing to eat it in the absence of sunflower seeds. In the winter, and as late as February when they were eating rat biscuit, it proved impossible to get good performances using rat biscuit pellets as food reward; they would quit after getting 30 or 40 pellets. Diet was varied with raw meat and fruit (both are eaten in the wild when available, though seeds are the staple diet) and cheese. Small bird seed was not popular.

Hibernation is a problem, and difficult to control since the factors leading to it are not well understood. In the windowless laboratory room, with controlled temperature (about 70 degrees) and a 12-hour light-dark, artificial light controlled cycle, with exercise wheels available, none of the squirrels really hibernated. Two that were not being used and getting fed ad lib seldom woke up during the winter; and of the four being used during the winter experiment, one slept most of the time and was too lethargic to perform well, another was somewhat lethargic, and the other two appeared normal. All four of these were on slightly short rations and had to work for most of what they did get. In the spring, all subjects were alert, active and hungry.

Golden mantled squirrels must be caged separately and prevented from escaping, which is not easy, to prevent fights and injury. Under natural conditions they are fiercely independent, never socializing on amicable terms, and two squirrels confined in a single cage or room is in my experience a sure recipe for a good fight; my best subject died following infection from a bite received in such a fight.

While these squirrels are occasionally available at pet stores, they are expensive. They're easy and interesting to trap, though they apparently occur in large concentrations only in campgrounds. One needs a much larger box trap than one would think, as they're quick enough to dash out of a short one before the door latches. Stinky bait (peanut butter, chocolate when it's a hot day, jam) seems to work best. Traps are best placed about two feet from burrow entrances; when they are closer, the squirrels often will not come out for a long time, and when placed at random it takes the squirrels a long time to find them. The best subjects were apparently yearlings or early spring young trapped in the fall. Two very young ones, obviously born late in the spring, proved too timid to work with easily; and a large, apparently fully adult animal was too fierce to work with. Sex is more difficult to determine except in the spring when the males' testes descend, but it apparently made little difference in the handleability of the subjects.