FRUIT COLOR CHOICES OF CAPTIVE SILVEREYES (*ZOSTEROPS LATERALIS*)[1]

HELEN L. PUCKEY, ALAN LILL[2] AND DENNIS J. O'DOWD[3]

Department of Ecology and Evolutionary Biology, Monash University, Clayton, Victoria 3168, Australia

Abstract. Fleshy fruits occur in many colors in nature, but red and black predominate. One popular hypothesis to explain the adaptive significance of fruit coloration is that it attracts frugivorous birds that disperse seeds. We presented Silvereyes (*Zosterops lateralis*), important fruit consumers in southern Australia, with choices in the aviary between both artificial fruits (made from gelatin) and actual fruits (*Rhagodia parabolica*) of three different colors (red, yellow and white). Silvereyes exhibited a strong overall preference for red among both artificial and real fruits. Although individual birds varied in their color preferences for artificial fruits, all preferred the red fruits of *R. parabolica*. The consumption rate of real fruits was much greater than that of artificial fruits, which was probably attributable to differences in the characteristics of the two fruit types. Exposure of Silvereyes to a maintenance diet of a particular color for 12 days also failed to alter their collective preference for red fruits. Further, responses to artificial infructescences offering color choices either between or within infructescences showed that Silvereyes preferred red fruits regardless of the spatial format of presentation. The overall fruit color preferences of Silvereyes were based on selection of hue rather than brightness, but within the same hue, some individuals exhibited preferences for particular brightness levels. These results are consistent with the hypothesis that fruit color is related to avian frugivory and suggest that birds can act as strong selective agents on fruit color.

Key words: brightness; color; frugivory; fruit-color polymorphism; fruits; hue; preference; Silvereye; Zosterops lateralis.

INTRODUCTION

Red is one of the most common colors of bird-dispersed fruits (Ridley 1930). Surveys of regional floras, despite their taxonomic differences, support this generalization (Turcek 1963, Knight and Siegfried 1983, Gautier-Hion et al. 1985, Wheelwright and Janson 1985, Lee et al. 1988, Willson et al. 1989). Willson and Whelan (1990) proposed a set of hypotheses to explain the evolution of fruit color. Of these, perhaps the most intuitively appealing hypothesis is that certain colors are more attractive to frugivorous birds and promote seed dispersal. However, only a few experiments have examined whether birds discriminate among fruits on the basis of color (Mc-Pherson 1987, 1988, Willson et al. 1990, Willson and Comet 1993, Willson 1994). Collectively, these studies showed that individual birds differ

in their initial color preferences, and in the transitivity and temporal stability of these preferences. Often, however, inferences about the importance of color in determining fruit preferences in aviary studies have been confounded by cross-species comparisons of fruits that introduce other, uncontrolled variables such as their size, shape, taste and nutritional value (Turcek 1963, Mc-Pherson 1987, Moermond et al. 1987). Further, in studies involving artificial "fruits", it is unclear whether their use reflects the birds' preferences for real fruits (Willson et al. 1990). Field-based studies on the influence of color on fruit selection are complicated by other factors such as crop size, accessibility, relative abundance, and differences in plant morphology (Wheelwright and Janson 1985, McPherson 1987, Willson and O'Dowd 1989, Whelan and Willson 1994).

Silvereyes (*Zosterops lateralis*, Zosteropidae) are major consumers of fleshy fruits in southern Australia, consuming fruits of just under half of the 100 or so plant species whose fruits are reported to be taken by birds in temperate Australia (Forde 1986, French 1990). We used aviary experiments to determine whether Silvereyes exhibit a distinct color preference in their selection

of fruits. First, we examined the strength and consistency of their fruit-color preferences over a short time scale, using both artificial fruits and the polymorphic fruits of the shrub, *Rhagodia parabolica* R.Br. (Chenopodiaceae). Second, because birds may learn quickly to change their preferences for fruits, depending on their degree of exposure to them and on their availability (Morden-Moore and Willson 1982), we exposed Silvereyes to a diet of a particular color to see if their fruit color preferences changed as a result. Third, the spatial scale at which fruit color selection might be made is poorly known. We examined the effect of scale of fruit presentation (within and between artificial infructescences) on the color preferences of Silvereyes. Lastly, we determined whether the fruit color preferences of Silvereyes were based on differences in hue or brightness, the two aspects that make up what we commonly refer to as color (Goldstein 1989).

METHODS

EXPERIMENTAL PROCEDURES

Twenty-seven adult Silvereyes were caught under permit in mist nets between 29 February 1993 and 7 January 1994 at Bacchus Marsh, approximately 53 km west of Melbourne, Victoria, Australia (37°37'S, 144°25'E). The birds were maintained in a holding aviary (approximately 3 × 2 × 2 m). They were given at least two weeks to adjust to captive conditions and were fed on a maintenance diet of Farex® baby food, apples, pears, and water. For all experiments, birds were placed in individual cages (37 cm wide × 50 cm deep × 36 cm high) and given an additional 5 days on the maintenance diet to adjust. These cages were placed together in a room such that the birds could not make visual contact, but could hear one another. Each cage had a wire mesh front that allowed access and observations to be made. Perches were placed at both ends of each cage and food was always presented at the front of the cage. On any test day, the birds were tested serially after being deprived of food for one hour; after the trial, each bird was placed on the maintenance diet again. Water was available ad libitum. The trials in any one experiment were carried out on consecutive days between 06:00–11:00. The time at which each bird was tested was varied systematically to test for any possible effect of time of day on fruit-color preferences. Like Moermond et al. (1986),

we determined preferences by the number of fruits of each color consumed and the order in which they were consumed. Once presented with the test fruits, each bird was observed at 2 m distance from behind a blind. Using an event recorder, we monitored the number of fruits of each color taken and the sequence in which they were removed over a specified time.

The use of gelatin-based, artificial fruits as well as the natural polymorphic fruits of Oldman Saltbush, *Rhagodia parabolica,* allowed us to compare color preferences involving different pigment systems and attempt to control for all factors other than color itself (Appendix 1). Genetically polymorphic fleshy fruits occur where different individuals of the same species produce fruits of different colors. Individual plants of *Rhagodia parabolica* produce red, yellow or white fruits and these color morphs do not differ significantly in size, mass, pulp-seed ratio, water content or major nutrients (Willson and O'Dowd 1989).

Artificial fruits were made from a sugar and gelatin recipe modified from Levey and Grajal (1991) and were dyed either red, yellow (using McKormick® food dyes) or white (using titanium white) to approximate the same color standards as the fruits of *R. parabolica* (approximate Methuen colors: 10B8, 3A7 and 1A1, respectively, Kornerup and Wanscher 1961). Fruits of *R. parabolica* were collected in January 1993 from remnant eucalypt mallee at Djerriwarrh Creek (Myers et al. 1986), approximately 11 km southeast of Bacchus Marsh. Fruits were frozen at −15°C to prevent deterioration and to enable experiments to be carried out when the fruits were not available in the field.

EXPERIMENT 1: COLOR SELECTION OF ARTIFICIAL AND REAL FRUITS

Fruit-color preferences of Silvereyes were first examined using artificial fruits and then fruits of *R. parabolica,* with an interval of approximately one week between test series. Fourteen birds were tested once daily for seven consecutive days, and in each trial all three fruit colors were presented simultaneously. Each trial lasted for 25 minutes. Three (10 cm diameter) glass petri-dishes were placed in a row on the floor at the front of the cage. This forced the birds to leave the perches to feed. Each dish contained 20 fruits of a single color. They were presented on a rectangular (34.5 × 10 cm) background of green cardboard (Me-

thuen 26E8) to approximate the contrast between the fruits and their background color in nature. The positions in which the different colored fruits were presented in each trial were selected randomly from the six different permutations possible to control for any effect of position.

EXPERIMENT 2: PREVIOUS COLOR EXPERIENCE

Fruit removal before and after exposure to a colored maintenance diet was compared to determine if previous experience affected fruit-color preferences. Fifteen Silvereyes were tested, 12 of which had been used previously in Experiment 1. Birds were fed on the standard maintenance diet in the aviary and test cage prior to the experiment. They were then given fruit-color preference tests with *R. parabolica* for 15 minutes each on four consecutive days. The birds were then divided randomly into three groups of four (the three birds that had not participated in Experiment 1 were allocated so that one was in each of the three groups). Over the next 12 days, one of the groups was fed on the original whitish maintenance diet, while the second and third groups were fed exactly the same maintenance diet, except that it had been dyed either red or yellow with McKormick® food dyes. After this period of exposure, the birds were re-tested for another four days.

EXPERIMENT 3: SPATIAL SCALE

Twelve experimentally naive Silvereyes were tested to determine if scale of presentation affects fruit-color choice. Artificial infructescences were constructed with florist's materials: green, plastic-coated wire "stems" and small green cloth "leaves". On each infructescence, 15 fruits of *R. parabolica* were mounted on the ends of the stems against a background of seven leaves. During trials, the infructescences were hung from the wire front of the cage, approximately 5 cm from the floor. The artificial infructescences were presented to Silvereyes in two ways. First, three infructescences, each with 15 fruits of a single color (red, yellow or white), were presented simultaneously in trials. In this way, birds effectively selected fruit colors by choosing among infructescences. Second, five fruits of each color were arranged haphazardly on each of the three infructescences such that birds selected fruit colors within infructescences. Each bird was tested daily for 15 minutes on four consecutive days on

the first type of presentation. The second type of presentation was then administered in the same way, after a one-day interval.

EXPERIMENT 4: HUE AND BRIGHTNESS

Using the same birds as in Experiment 3, we examined whether the apparent color preferences of Silvereyes are based on hue or brightness. Hue is determined by the spectral composition of the light reflected from the stimulus. Brightness, or luminance, is determined by the total amount of energy over all wavelengths reflected from the stimulus. If a bird, presented with its preferred fruit color in conjunction with a series of gray fruits, ranging from white to black, still takes its favored color, it responds to hue as such (Muntz 1974). A series of artificial fruits were made from the gelatin recipe by adding different amounts of black and white food dye to approximate a gray scale of 0%, 25%, 50%, 75%, and 100% of black. Measurement with a photographic spot-meter (Calculight®) gave relative $\log_{10}$ values of luminance for the fruits of 1.00, 0.63, 0.32, 0.20, and 0.06, respectively. Thus, these fruits differed in brightness, but not hue. Red artificial fruits of two brightness levels (0.06 and 0.10 $\log_{10}$ values as measured with the spot-meter) were also used to control for the possibility that the birds may select fruits on absolute brightness values. Ten artificial fruits were placed in each of seven (50 mm diameter) plastic petri-dishes, such that each dish contained only one fruit type. Petri-dishes were assigned randomly to positions. Each bird was tested daily for 15 minutes over four consecutive days.

STATISTICAL ANALYSES

The simplest and most conservative way to assess the preferences of Silvereyes when all fruits were equally available was to record only the color of the first fruit taken in each trial (Table 1). However, fuller insight can be gained by considering the number of fruits taken over some or all of the trial. The counts were analyzed with a log-linear model assuming that the errors were Poisson distributed. The log-likelihood ratio statistic (LRS) was used to assess the fit of the model and to test any hypotheses using GLIM (General Linear Interactive Modelling, see Aitkin et al. 1987, Crawley 1993). The LRS is chi-square distributed (Aitkin et al. 1987).

Two inherent biases in the data were caused by the tendency for fruit of a particular color to

TABLE 1. Fruit-color preferences based on the first fruit consumed by Silvereyes in each trial. Proportions are based on the number of trials in which a particular color was consumed first. Values in parentheses are the total number of trials. Experiments are listed in chronological order. Birds that did not respond to fruits are excluded.

Experiment	Proportion of first fruits consumed			No. birds; trials/bird
	Red	Yellow	White	
1a. Artificial fruits	0.62	0.06	0.32	11; 7 (77)
1b. R. parabolica	0.85	0.09	0.06	13; 7 (91)
2. Previous exposure				
Pre	0.77	0.08	0.15	15; 4 (60)
Post	0.70	0.13	0.17	15; 4 (60)
3. Spatial scale				
Within infructescence	0.73	0.04	0.23	12; 4 (48)
Between infructescence	0.69	0.12	0.19	12; 4 (48)

be taken in runs and by fruit depletion. A bird already perching on a dish is more likely to take fruit from that dish than to move to another one. Thus, the trials tend to result in clustering ("overdispersion") of data. This can be overcome with GLIM by introducing a scaling factor, found by dividing the residual deviance by the residual degrees of freedom (Aitkin et al. 1987). The analysis is first run as a Poisson model and then the scaling factor is derived and the model re-run. Because we did not replace fruits removed by birds, the probability of taking the favored color necessarily decreased during the trial. This would decrease the likelihood of detecting a real preference. Except in Experiment 4, a cut-off point when 50% of fruits had been taken was therefore used, rather than a specified elapsed time, because birds depleted fruits at different rates. A lower cut-off point would tend to exclude information about the frequencies at which the less preferred fruits were taken.

Preferences are expressed as the number of fruits of different colors consumed in the feeding trials or as a rank based on the relative proportions in which the different fruits were consumed. GLIM analyses indicate the significance of effects and interactions and, by inspection of the data, we can rank the colors in a preference order. Box plots (Wilkinson 1990) rather than means ($\pm$ SE) are used to graphically portray the results, because the distributions of fruit removal were non-normal and had heterogeneous variances.

RESULTS

EXPERIMENT 1: SELECTION OF ARTIFICIAL AND REAL FRUITS

Given a choice between red, yellow or white artificial fruits, Silvereyes showed an overall pref-
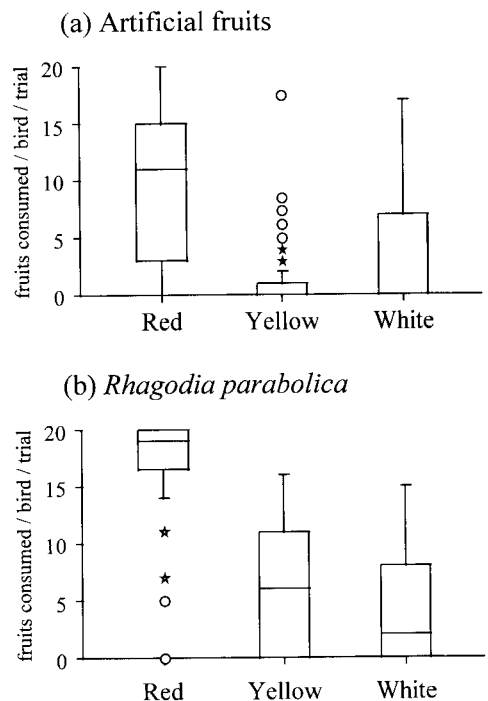

FIGURE 1. Boxplots of the number of fruits of each color taken by Silvereyes per trial for (a) artificial fruits (excluding three birds that did not respond to the test fruits) and (b) fruits of Rhagodia parabolica (excluding one non-responding bird). The boxplot shows the median (cross bar in open box) and 25% quartiles (represented by each end of the box). The length of the entire box or "spread" represents the interquartile range. The line extending from each end of the box encompasses all values within a range beyond the 25% quartile that is 1.5 times the spread. The stars represent outliers and open circles represent far outside values (see Wilkinson 1990).

TABLE 2.   GLIM analysis of the color preferences of Silvereyes for both the artificial fruits (excluding three non-responding birds) and the fruits of *Rhagodia parabolica* (excluding one non-responding bird). Analyses were based on the first 50% of fruits (30 fruits) consumed by individual Silvereyes in each trial. ns = $P > 0.05$.

Source	Artificial fruits			R. parabolica		
	x^2	df	P	x^2	df	P
Bird	17.0	10	ns	13.5	12	ns
Color	275.0	2	< 0.001	520.9	2	< 0.001
Day	2.2	1	ns	4.5	1	< 0.05
Bird × day	5.3	10	ns	13.8	12	ns
Color × bird	376.3	20	< 0.001	240.4	24	< 0.001
Color × day	18.4	2	< 0.01	3.5	2	ns
Bird × color × day	51.3	20	< 0.001	58.7	24	< 0.001

erence ranking of R>W>Y (Fig. 1a). This preference for red was highly significant (color effect, Table 2) and was consistent with the strong preference for red observed when only the first artificial fruit consumed in each trial was considered (Experiment 1a, Table 1). Still, a few birds deviated in either their color preference or in the consistency of their preferences over the 7-day period (color × bird, color × bird × day interactions; Table 2). Of the 11 of 14 birds that consumed artificial fruits, eight preferred red and three preferred white.

Silvereyes showed an overall preference ranking of R>Y>W when given the same color choices of natural *R. parabolica* fruits (Fig. 1b). This preference for red was highly significant (color effect, Table 2) and consistent with the strong preference for red apparent when only the first fruit consumed in each trial was considered (Experiment 1b, Table 1). Although the 13 responding birds all preferred red fruits, individual Silvereyes differed in the relative strength of their preferences for yellow and white (color × bird interaction, Table 2).

For both fruit types, neither time of day at which the birds were tested (for artificial fruits, $x^2 = 3.7$, df = 6, $P > 0.05$; for *R. parabolica*, x^2

= 2.8, df = 6, $P > 0.05$) nor dish position (for artificial fruits, $x^2 = 1.4$, df = 5, $P > 0.05$; for *R. parabolica*, $x^2 = 1.5$, df = 5, $P > 0.05$) had any significant effect on fruit color choice.

EXPERIMENT 2: PREVIOUS COLOR EXPERIENCE

Following exposure to a maintenance diet of a single color (either red, yellow or white) for 12 consecutive days, Silvereyes showed no significant overall change in their color preferences (color × pre/post interaction, Table 3) and still chose red fruits of *R. parabolica* (Fig. 2). This was consistent with analyses based on the first fruit consumed (Experiment 2, Table 1). Groups exposed to white and yellow maintenance diets both showed a fruit color preference ranking of R>W>Y before and after exposure to the diet (Fig. 2a,b). For Silvereyes exposed to a red maintenance diet, preferences ranked R>Y>W pre- and post-exposure (Fig. 2c). These differences in rankings of white and yellow fruits were reflected in the significant interaction between color and exposure group (Table 3). However, no difference was found for any group in the number of fruits of each color eaten before and after they were exposed to a particular colored mainte-

TABLE 3.   GLIM analysis of the effects of exposure to a single-colored maintenance diet on the color preferences of Silvereyes for fruits of *Rhagodia parabolica*. ns = $P > 0.05$. Analyses were based on the first 50% of fruits (30 fruits) consumed by individual Silvereyes in each trial.

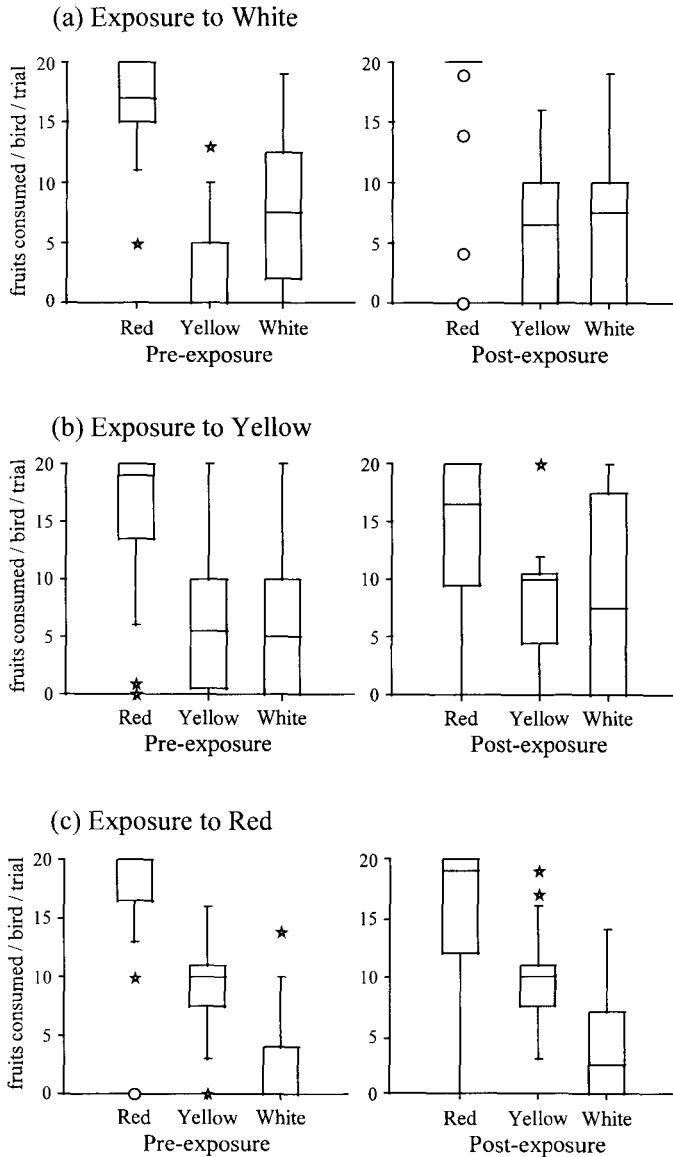| Source	x^2	df	P
Color	138.52	2	< 0.001
Pre/post exposure	0.73	1	ns
Exposure group	0.17	2	ns
Color × pre/post	2.47	2	ns
Color × exposure group	33.98	4	< 0.001
Pre/post × exposure group	0.29	2	ns
Color × pre/post × exposure group	6.30	4	ns

FIGURE 2.   Boxplots of the numbers of red, yellow and white fruits of *Rhagodia parabolica* taken by Silvereyes pre- and post-exposure to a (a) white maintenance diet, (b) yellow maintenance diet, and (c) red maintenance diet.

nance diet (color × pre/post × exposure group interaction, Table 3).

EXPERIMENT 3: SPATIAL SCALE

Scale of presentation of *R. parabolica* fruit did not affect the overall color preferences of Silvereyes. In both choice situations (between and within infructescences), red was preferred, followed by white and then yellow fruits (Fig. 3).

This order was also apparent in the color of the first fruit consumed in each trial (Experiment 3, Table 1). Analyses showed a significant overall color preference (color effect, Table 4), but no significant difference in the color preferences in the two choice situations (color × between/within interaction, Table 4). However, some individual birds showed significantly different color preferences in the two presentation types (bird

(a) Within infructescences
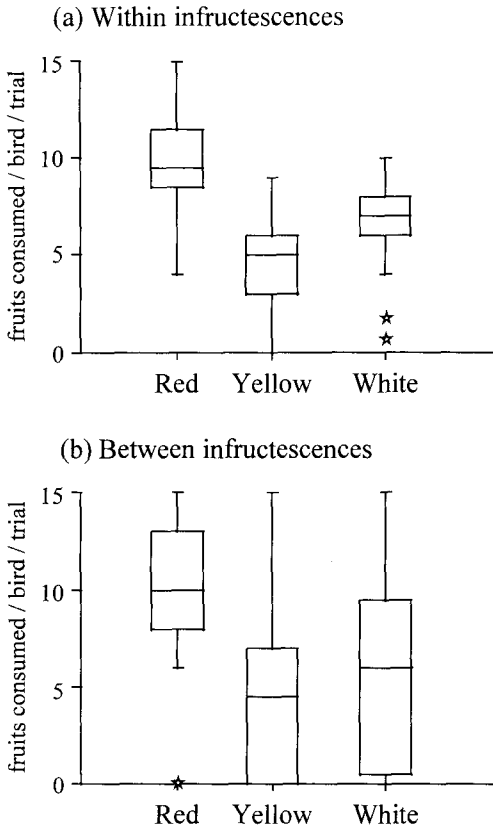

(b) Between infructescences

FIGURE 3. Boxplots of the numbers of red, yellow, and white fruits of *Rhagodia parabolica* taken by Silvereyes per trial (excluding one non-responding bird) when the choice of colors was presented either (a) within or (b) between artificial infructescences.

$\times$ color $\times$ b/w interaction, Table 4). Of the 11 birds that took fruits, seven showed a consistent preference for red fruits, irrespective of scale of presentation. Three birds preferred red fruits at the within-infructescence scale but white fruits between infructescences; one individual took more red fruits at the within-infructescence scale, but more yellow from the other format.

EXPERIMENT 4: HUE AND BRIGHTNESS

Silvereyes selected fruits on the basis of hue rather than brightness. Given a choice of artificial fruits of five brightness levels of gray and two brightness levels of red, the birds exhibited a strong overall preference for red. Of the 11 birds that consumed fruits, 10 ate red fruits of both brightness levels almost exclusively, and one ate white fruits and the gray fruits closest to them

TABLE 4. GLIM analysis of the preferences of Silvereyes for fruits of *Rhagodia parabolica* at two different spatial scales (within and between infructescences). One bird was not included in the analysis because it did not take fruits in either situation. ns = $P > 0.05$. Analyses were based on the first 50% of fruits (22 fruits) consumed by individual Silvereyes in each trial.

Source	χ^2	df	P
Bird	8.12	11	ns
Between/within	0.25	1	ns
Day	1.17	3	ns
Color	106.57	2	< 0.001
Bird $\times$ between/within	2.16	11	ns
Bird $\times$ day	5.57	33	ns
Color $\times$ between/within	0.95	2	ns
Day $\times$ color	13.01	6	< 0.05
Bird $\times$ color $\times$ b/w	132.40	44	< 0.001

in brightness (Fig. 4). This result was reflected in the proportions of fruits removed first. In 92 percent of trials, Silvereyes took red fruits first; in the others, white was chosen first. We only analyzed variation in the number of red fruits of each brightness level consumed because Silvereyes took few other fruits. Brightness had no significant overall effect on removal of these red fruits ($\chi^2 = 0.1$, df = 1, $P > 0.05$, brightness level); this was consistent with the proportions of fruits consumed first by Silvereyes, namely 50% and 42% for higher and lower brightness levels of red fruits, respectively. However, individuals varied in their preferences for different shades of red ($\chi^2 = 31.7$, df = 10, $P < 0.001$, bird $\times$ brightness interaction). There was no significant daily variation in fruit removal ($\chi^2 = 1.8$, df = 3, $P > 0.05$, effect of day) or in the total number of fruits eaten by individual birds in each trial ($\chi^2 = 4.6$, $P > 0.05$, bird $\times$ day interaction).

DISCUSSION

CONSISTENCY IN FRUIT COLOR SELECTION

Red color was important in the fruit choices of Silvereyes in our aviary experiments. First, red was preferred overall for both artificial and *R. parabolica* fruits (Experiment 1), even though the actual pigments of the fruit types differed. Second, the attraction of Silvereyes to red fruits was not altered by exposure to a particular colored maintenance diet (Experiment 2). Third, Silvereyes preferred red fruits regardless of the spatial scale (within and between infructescences) or mode of the presentation (petri dish or infruc-
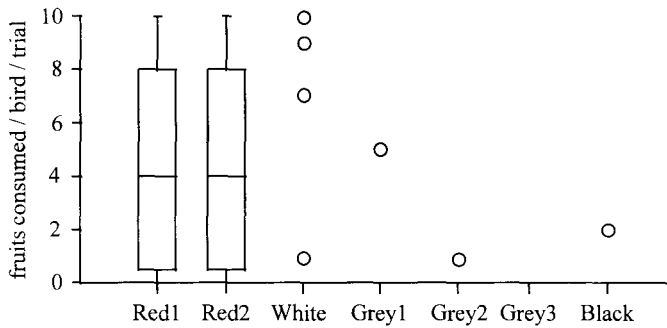
FIGURE 4. Number of artificial fruits taken by Silvereyes per trial when given a choice of two brightness levels of red (1 and 2) and five shades of gray (including black and white). Data are for the entire 15 minute trials.

tescence) employed (Experiment 3, Experiment 1 vs. Experiment 3). Together, these experiments show a temporal and spatial consistency in color selection not reported in aviary studies of other frugivorous birds. Captive Northwestern Crows (*Corvus caurinus*) and American Robins (*Turdus migratorius*) exhibited considerable individual variation in their color preferences when presented with red, blue, yellow, and green artificial fruits (Willson and Comet 1993, Willson 1994). Cedar Waxwings (*Bombycilla cedrorum*) initially showed a clear preference for red artificial fruits over blue, green, and yellow ones, but fed more equally on all colors as the tests progressed (McPherson 1988). Evidence for an overall color preference when offered red, blue, yellow and black artificial fruits was not strong among Gray Catbirds (*Dumetella carolinensis*), Swainson's Thrushes (*Catharus ustulatus*) or Hermit Thrushes (*C. guttatus*) (Willson et al. 1990).

Individual variation in color preferences among Silvereyes was greater with the artificial fruits than with *R. parabolica* fruits, for which all birds preferred red. If artificial fruits are "sub-optimal" stimuli, individual differences in the preferences of birds might be more apparent than with the fruits of *R. parabolica*. In fact, the lower consumption rates of artificial fruits (Fig. 2, a vs. b) is consistent with this explanation; different tastes, sizes, texture and nutritional rewards of the two fruit types could explain the disparity. Similarly, differences in familiarity of Silvereyes with the two fruit types may have affected the handling effort required to consume the fruits. Nevertheless, the overall color preferences of Silvereyes when presented with artificial fruits generally reflected those shown between real fruits in these experiments.

The suggestion that frugivorous birds can quickly change their fruit-color preferences depending on exposure (Morden-Moore and Willson 1982) was not supported in our study. Therefore, Silvereyes' fruit-color preferences probably were not affected by experience with particular fruit colors prior to capture. The use of white as an exposure color in one group of birds controlled for any effect of previous experience with the white maintenance diet used throughout the period of captivity. Willson and Comet (1993) found that groups of nestling Northwestern Crows hand-raised on single-colored diets (either red, yellow or "neutral") did not necessarily select the fruit color on which they were raised. This, together with our findings, suggests that experience with, or exposure to particular food colors may not strongly affect fruit color preferences. In our study, exposure to a particular colored maintenance diet may not have lasted long enough to affect fruit color preferences. However, longer exposure times for crows (Willson and Comet 1993) did not alter color preferences consistently. Furthermore, if Silvereyes made no association between maintenance diet color and test fruit color because of the disparity in these foods, then exposure would understandably have had no effect on fruit choices. It may be necessary to expose the birds to actual fruits of a particular color prior to testing for any effect of exposure on color preferences among such fruits.

It seems surprising that generalist frugivores like Silvereyes should show such strong and consistent preferences for red fruits in the aviary, when they feed on fruits of many colors in the field (Forde 1986, French 1990). Indeed, the relative removal rates of the different fruit color morphs of *R. parabolica* in the field, where Sil-

vereyes were the major frugivore, were not markedly different (Willson and O'Dowd 1989). The apparent discrepancy between the fruit color morphs preferred by Silvereyes in the aviary and in the field suggests that either multiple factors affect color selection of *R. parabolica* or that more rigorous field tests are required. Among the fruit colors we examined, red may be preferred because it is highly conspicuous, i.e., contrasts strongly with background color. In the genus *Coprosma*, reddish fruit colors show more contrast against green leaves than other fruit-color groups (Lee et al. 1994). In nature, color may serve as a conspicuous cue or "orienting stimulus" that guides seed dispersers to a valuable food resource (McPherson 1988, Willson and Whelan 1990, Willson 1994).

BASIS OF COLOR SELECTION

Silvereyes selected fruit colors on the basis of hue rather than brightness (Experiment 4). Birds in general are thought to have well-developed color vision, especially within the orange-red part of the spectrum (Burkhardt 1982), and a few experiments have demonstrated color vision in pigeons and domestic chickens (Kare and Rogers 1976). To our knowledge, this is the first study to provide evidence that fruit-color choice by any frugivorous bird is based on hue. The results of surveys of the colors of bird-dispersed fruits and of many experiments on fruit color choice in birds have been assumed on the basis of hue alone. If Silvereyes had selected fruits on the basis of brightness in Experiment 4, some important inferences about color preference drawn in previous studies might have required re-evaluation. Certainly, more studies on a variety of frugivorous species need to be carried out, because it is unlikely that all frugivorous birds select fruit color on the same basis. Although Silvereyes selected fruits primarily on the basis of hue, some individuals appeared capable of recognizing differences in brightness and responding to them.

Pigments are not necessarily without flavor, and different tastes associated with them might account for the observed color preferences of Silvereyes. We could not distinguish differences in flavor among artificial fruits of different colors or among the polymorphic fruits of *R. parabolica*, although the birds may have been able to do so. We attempted to evaluate the possibility that taste was a confounding variable in fruit color choice by using different pigment systems. That the overall color preferences for artificial and real fruits were similar suggests that pigment flavors were unlikely to explain fruit-color preferences in our experiments.

Wheelwright and Janson (1985) suggested that studies of fruit color within plant genera may yield clearer ecological correlates than investigations involving unrelated taxa. Genetic fruit-color polymorphisms may provide an even more powerful experimental tool because other fruit traits are more likely to be similar among color morphs. These polymorphisms are widespread, occurring in a variety of plant species in many different habitats (Willson 1986, Lee et al. 1988, Willson and O'Dowd 1989). Unfortunately, to date only a few aviary studies have yet examined avian color preferences among polymorphic fruits, and, except for our study, none has shown consistent patterns of selection among color morphs (Willson and Comet 1993, Willson 1994). Interestingly, the preference of captive Silvereyes for the red fruits of *R. parabolica* in our study paralleled their high frequency in the field relative to white and yellow color morphs (Willson and O'Dowd 1989).

Our results support the hypothesis that red fruit coloration is an adaptation for promoting avian frugivory and seed dispersal (Willson and Whelan 1990). Although this study examined preferences of only one species of frugivorous bird feeding on just two fruit types, the strong preference for red was consistent with the high frequency and conspicuousness of red fruits reported in nature.

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APPENDIX 1. Selected characteristics of artificial fruits and polychromatic fruits of *Rhagodia parabolica* used in all preference trials. For *R. parabolica,* the mean is followed by SE in parentheses (data from Willson and O'Dowd 1989). SE is not given for artificial fruits as they were made to the same recipe (except for the pigments) and in the same fruit molds.

Trait	Artificial fruits			*Rhagodia parabolica*		
	Red	Yellow	White	Red	Yellow	White
Pigments	azorubine tartrazine	tartrazine ponceau-4R	titanium dioxide	betacyanins	betaxanthins	flavonoids
Diameter (mm)		6.5		3.2 (0.05)	3.2 (0.07)	3.4 (0.06)
Sugars (% dry mass)						
Fructose		32.6		21.3 (0.6)	25.5 (0.5)	23.3 (0.5)
Glucose		32.6		23.5 (0.4)	28.7 (0.4)	22.8 (1.3)
Sucrose		0		7.3 (0.5)	4.7 (0.3)	5.3 (0.3)
Total		65.2		53.7 (1.6)	58.1 (0.4)	49.4 (1.9)
Gelatin (% dry mass)		34.8		—	—	—
Water (%)		81.3		79 (0.3)	77 (0.6)	76 (0.6)