







**Table 1.** Female Capuchin Color Vision Phenotypes, Survivorship, and Production of Infants. M-L pigment sensitivity describes the peak spectral sensitivity ( $\lambda_{\max}$ ) of the constituent middle-to-long wavelength sensitive photopigment(s) (red = 561 nm, yellow = 543 nm, green = 532 nm).

Animal ID	Color Vision Phenotype	M-L Pigment sensitivity(ies)	Age at Departure (years)	Depart Type	# of Offspring	mean IBI <sup>a</sup> (years)	mean IBI <sup>b</sup> (years)
BAL	Dichromat	Red	9.55	End of Study	1		
CHA	Dichromat	Red	8.05	End of Study	1		
ED	Dichromat	Red	12.52	End of Study	5	2.34	0.93
KIA	Dichromat	Red	10.56	End of Study	2	2.88	
LIM	Dichromat	Red	22.05	Death	8	2.21	0.67
NEM	Dichromat	Red	8.69	End of Study	1		
NYL	Dichromat	Red	11.11	Death	4	1.83	1.16
PIC	Dichromat	Yellow	9.60	End of Study	2	2.06	
PUM	Dichromat	Red	10.59	End of Study	3	1.95	
SAR	Dichromat	Red	11.88	End of Study	3	1.86	
SER	Dichromat	Red	23.44	End of Study	7	2.26	
SHA	Dichromat	Red	9.71	End of Study	2	3.04	
SHE	Dichromat	Red	3.58	Death	0		
SIM	Dichromat	Red	14.29	End of Study	4	2.06	
TIM	Dichromat	Red	16.51	End of Study	4	1.93	
ZAZ	Dichromat	Red	13.80	End of Study	3	2.56	
ROS	Dichromat	Red	19.37	Death	2	1.49	
RIT	Dichromat	Red	12.88	End of Study	3	1.96	
FAW	Dichromat	Yellow	1.21	Death	0		
QUI	Dichromat	Red	5.55	End of Study	0		
GAI	Dichromat	Yellow	4.36	End of Study	0		
ABU	Trichromat	Green/Red	7.57	End of Study	0		
BLA	Trichromat	Green/Yellow	26.75	Death	10	2.05	1.02
CHU	Trichromat	Yellow/Red	13.30	End of Study	5	2.24	0.90
DOS	Trichromat	Green/Red	20.15	Death	8	1.77	1.01
KAT	Trichromat	Yellow/Red	23.19	Death	11	1.83	0.88
MAY	Trichromat	Yellow/Red	6.20	Death	1		
ORE	Trichromat	Green/Red	7.61	End of Study	1		
SAL	Trichromat	Green/Yellow	16.72	End of Study	6	1.83	
VEL	Trichromat	Green/Red	6.22	Death	0		
BEA	Trichromat	Green/Red	6.69	End of Study	0		
ARI	Trichromat	Green/Red	6.45	End of Study	0		
PAN	Trichromat	Green/Red	2.35	Death	0		
MIN	Trichromat	Green/Yellow	22.88 <sup>c</sup>	End of Study	3	2.27	1.69
MAX	Trichromat	Yellow/Red	19.81 <sup>c</sup>	Death	3	1.80	
LUN	Trichromat	Green/Yellow	22.88 <sup>c</sup>	End of Study	3	2.05	1.84
FLE	Trichromat	Green/Red	15.88 <sup>c</sup>	End of Study	3	2.08	
LIL	Trichromat	Yellow/Red	15.88 <sup>c</sup>	End of Study	4	2.67	0.99
PET	Trichromat	Green/Red	13.88 <sup>c</sup>	End of Study	3	2.61	
MRS	Trichromat	Green/Red	18.88 <sup>c</sup>	End of Study	6	2.21	0.98
PAD	Trichromat	Green/Yellow	9.88	End of Study	1		
CHO	Trichromat	Green/Red	9.35	Death	2		0.74
ATH	Trichromat	Yellow/Red	12.14 <sup>c</sup>	Death	3	3.16	
ELE	Trichromat	Green/Yellow	13.88 <sup>c</sup>	End of Study	3	1.95	
CAL	Trichromat	Green/Red	11.88 <sup>c</sup>	End of Study	5	1.65	0.78
HEL	Trichromat	Yellow/Red	9.88	End of Study	3	2.05	1.00
CRE	Trichromat	Green/Red	2.77	Death	0		

**Table 1. Cont.**

Animal ID	Color Vision Phenotype	M-L Pigment sensitivity(ies)	Age at Departure (years)	Depart Type	# of Offspring	mean IBI <sup>a</sup> (years)	mean IBI <sup>b</sup> (years)
THY	Trichromat	Green/Red	4.47	End of Study	0		
CAS	Trichromat	Green/Red	2.97	Death	0		

a = Mean of uncensored (complete) IBIs when the first infant in the interval lived  $\geq$  one year of age.

b = Mean of uncensored (complete) IBIs when the first infant in the interval died < one year of age.

c = entered study as an adult or subadult, age estimate based on morphological features at first sighting in 2007.

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allele), AB193778 (P543 allele) and AB193784 (P532 allele). Amino acid residues at the three critical tuning sites (exon 3, site 180; exon 5 sites 277 and 285) were determined to assign the color vision genotype [26]. We minimized the chances of allelic dropout by requiring that at least one fecal sample from each female contained no less than 200 pg of genomic DNA. Further details, including our PCR and sequencing protocols, are described in previous publications [24,26].

### Measures of Fitness and Reproductive Success

The rate of infant production (fertility) and survival of those infants, and longevity of the mother herself, are three important components of female fitness [38,47,48]. We address these three variables in turn.

In iteroparous organisms that habitually give birth to one infant at a time (most primates), fertility rates depend on the length of time between parturition events, i.e., the interbirth interval, or IBI [49]. We calculated the intervals between live births as our measure of fertility rate. IBIs are commonly used in primatology as a proxy for the number of infants born per female in a given time interval [38,50], and since our data on births were unavoidably constrained by the arbitrary start and stop dates of our study, it was more appropriate to use IBIs rather than number of infants born as our measure of female fertility. We included in our analyses intervals that were right censored by the stop date of our study or death/departure of the mother, since their exclusion may result in systematic bias toward shorter intervals [51]. Furthermore, our previous finding that death of an infant prior to 1 year of age shortens the length of the interbirth interval [39] led us to distinguish between intervals in which the first infant died prior to the age of 1 year and those in which the first infant survived. By separating out IBIs in which the first infant died prematurely, we were also able to remove any effects of early infant death/infanticide on IBI length.

To be reproductively successful, a female primate needs not only to produce infants but also to experience high rates of survival in her offspring and to live a comparatively long life herself. We examined the survival of a female's infants from their births to two years of age. We used age two as the cut-off point for calculating offspring survival on the assumption that prior to this age, an immature monkey's survival would be primarily a function of their mother's rather than their own color vision phenotype. This is because in the first year or two of life, prior to weaning, a young capuchin depends on its mother for milk and because the mother's ecological fitness and health determine the availability of her milk and the amount of care (e.g., transportation) and protection she can provide to the infant.

Our second measure of survival was that of the mother herself (longevity) which we calculated from two years of age (i.e. post-weaning) until her death or the end of our study. Sometimes we find the cadaver of a deceased study animal on the forest floor, or

we observe them to be wounded or ill before they disappear, in which case we record them as dead. Females seldom disperse (~12% of females have emigrated out of, or immigrated into our study groups) and in the few cases where females have dispersed from our study groups, we have tracked them to a neighboring group. Therefore, we assume that any cases of post-weaning female disappearances are deaths.

For both IBIs and the survival of infants, we accounted for potential autocorrelations in the fitness events experienced by each particular mother by introducing a random effect of the identity of the mother in the analyses. As noted by Jones et al. [49], introducing the random effect of the mother's identity also provides an indirect measure of "phenotypic quality" or "frailty."

### Statistical Analyses

To assess the pace of infant production, we used mixed effects Cox regressions (coxme and coxph procedures) [52] in R [53] and analyzed the length of 139 interbirth intervals (IBIs, Table 1). There were a total of 101 complete/uncensored and 38 censored intervals for 37 mothers of known visual phenotypes. The model included IBI as the dependent variable, a fixed effect of the mother's color vision phenotype (dichromatic or trichromatic), a fixed effect of whether the first infant in the interval died prior to age 1, and a random effect of the identity of the adult female. Censored values included cases where the female was still alive at the end of the study but had not yet given birth to another infant and cases where a female had died. Thus, if a female had N births, there were N values for IBI, the first being the interval between births 1 and 2, and the last being the censored interval between last birth and death/end of study.

To determine the effect of the mother's color vision type and of the mother's identity on the survival of her infants, we used mixed effects Cox regressions (combining coxme and coxph procedures) in R to analyze the survival of infants from birth to age 2. We included all 139 infants born to 37 females with known color vision phenotypes (Table 1). The model included age of the infant at death or at the end of the study if the infant was still alive but less than 2 years of age, as well as a fixed effect of the mother's color vision type and a random effect for the identity of the adult female.

To examine the longevity of trichromatic versus dichromatic females, we used a Cox proportional hazard regression (the coxph procedure in R) to analyze the survival of individual females from the age of two years on. There were a total of 48 females included in this analysis for which we know their color vision phenotype and that they survived beyond two years of age (Table 1). The model included a survival function for the females as a function of being trichromatic or dichromatic. The age at death was right-censored for those individuals still alive at the end of the study. The age of entry into the study was left censored if the individual did not enter the study at birth (in which case we estimated her age, based on age-related morphological features such as brow and nipple

length, and based on 26 years of observing the aging process in females of known age).

Because the advantage proposed to exist for trichromats is hypothesized to be particularly strong for those that have maximum sensitivity near the green or red end of the spectrum, we repeated all three analyses (IBI, offspring survival, maternal survival), using only reproductive data from Green/Red trichromats and comparing them to dichromats.

## Results

### Interbirth Interval Duration in Trichromatic versus Dichromatic Females

We examined the length of interbirth intervals (IBIs;  $N = 139$ ) as a function of the effect of: (1) the mother's color vision phenotype; (2) the death of the first infant in the interval at  $<1$  year of age; and (3) the random effect of the mother's identity. The interbirth intervals of trichromatic versus dichromatic females did not differ significantly ( $\chi^2 = 0.445$ ,  $df = 1$ ,  $p = 0.504$ , Figure 2). For IBIs where the first infant in the interval lived at least one year, the fitted median IBI was 2.05 years ( $N = 56$ ) for trichromatic females and 2.19 years ( $N = 45$ ) for dichromatic females.

In accordance with a previous study [39], we found that interbirth intervals in which the first infant died before age 1 were significantly shorter than intervals in which the first infant survived ( $\chi^2 = 59.5$ ,  $df = 1$ ,  $P < 0.001$ ) and this was true for both trichromats and dichromats (Figure 2). For IBIs where the first infant in the interval died before age 1, the fitted median IBI was 1.01 years ( $N = 28$ ) for trichromatic females and 1.13 years ( $N = 10$ ) for dichromatic females.

Finally, we found that the individual identity of the mother (i.e., the random effect of the mother independent of her vision phenotype) contributed significantly to the explanatory power of the model ( $\chi^2 = 4.460$ ,  $df = 1$ ,  $p = 0.035$ ).

### Survival of Infants Born to Trichromatic versus Dichromatic Mothers

We assessed the survival of infants ( $N = 139$ ) from birth to the age of two years, the typical timing of weaning, as a fixed effect of the mother's color vision phenotype and the random effect of the mother's identity. Infants of trichromatic mothers did not live longer (up to two years) than those born to dichromatic mothers ( $\chi^2 = 1.49$ ,  $df = 1$ ,  $p = 0.221$ ), nor did the identity of the mother contribute to explaining variation in the probability of the offspring surviving to the age of two ( $\chi^2 = 0.005$ ,  $df = 1$ ,  $p = 0.940$ , Figure 3). For trichromatic females, 61.9% of their offspring survived to age 2, whereas for dichromatic females, 79.6% of their offspring survived to age 2.

### Survival of Trichromatic versus Dichromatic Females Post Weaning

When we examined the survival of females past the age of 2 years as a function of their color vision phenotype we found that survival did not differ between trichromats and dichromats ( $\chi^2 = 0.91$ ,  $df = 1$ ,  $p = 0.339$ , Figure 4). The median predicted survival time for dichromatic females was 22.1 years ( $N = 20$ ) and 19.8 years for trichromats ( $N = 28$ ). Additionally, if we consider only those females who actually died before the end of our study, we can see from Table 1 that they lived between 1.21 and 26.75 years. The mean age of survival for the trichromatic females who died before the end of the study ( $n = 11$ ) was 11.99 years and the mean age of survival for dichromatic females who died ( $N = 5$ ) was 11.46 years.

### Comparison of Green/Red Trichromats to Dichromats for Interbirth Intervals, Offspring Survival and Maternal Survival

Because the L/M photopigments of Green/Yellow and Red/Yellow trichromats are less spectrally-separated (equivalent to "anomalous" trichromacies in humans) than the photopigments of Green/Red trichromats, it is possible that the former phenotypes might experience lower fitness and bring down the trichromatic group mean. To test for this, we performed the same analyses as those presented above, but this time we limited the sample of trichromats to the Green/Red phenotype.

We found that the results for all of these analyses were qualitatively identical to those presented above for the trichromat-dichromat comparison. There were no significant differences between Green/Red trichromats and dichromats on any of our three measures of female fitness. Specifically, the phenotype of the mother (Green/Red trichromat versus dichromat) has no discernible effect on the length of her IBI ( $\chi^2 = 1.41$ ,  $df = 1$ ,  $p = 0.234$ ), and the early death of the first offspring in an IBI leads to a shorter IBI for both Green/Red trichromats and dichromatic mothers ( $\chi^2 = 34.0$ ,  $df = 1$ ,  $p < 0.001$ ). Second, the mother's vision phenotype does not affect the offspring's survival up to 2 years ( $\chi^2 = 2.54$ ,  $df = 1$ ,  $p = 0.109$ ). Third, the survival of females after the age of 2 is not significantly affected by their vision phenotype ( $\chi^2 = 3.66$ ,  $df = 1$ ,  $p = 0.055$ ) and the trend is in the direction of dichromats surviving better than the Green/Red trichromats.

## Discussion

Although heterozygote superiority appears from the literature to be a widely accepted mechanism explaining primate color vision polymorphism, we found no significant advantage to trichromats over dichromats for the three measures of fitness we examined in female monkeys. Not only did the differences fail to reach significance, the trends for infant and maternal survival were in the opposite direction than predicted by the heterozygote superiority hypothesis (Figures 3 & 4). The one clear and consistent prediction from the literature is that Green/Red trichromats should experience visual advantages (and therefore fitness advantages) in comparison to the five other phenotypes found in capuchins, and in particular Green/Reds should do better than the dichromats [54–60]. However, even when we limited our analyses to the Green/Red trichromat females, there was no indication whatsoever that green/red trichromatic females do better than dichromats on any measure of fitness (fertility rates, offspring survival, maternal survival). We suggest therefore that an alternate selective mechanism is operating to maintain color vision polymorphism in our study animals.

Despite the lack of fitness differences due to color vision phenotype, we did find significant variation in IBIs attributable to the mother's identity, indicating that some aspect of phenotypic quality, other than color vision, is influential in the pace of infant production in our capuchins. These results are in accordance with other recent studies on female primates (e.g., 49]) in which the effect of the mother's identity was investigated. Dominance rank and age are unlikely to explain these characteristic IBI lengths that are consistent over a female's lifetime, in particular because rank and age change over the course of a female capuchin's life and because our previous studies of the effects of dominance and age failed to demonstrate that these variables are significant predictors of IBI length in our study animals [39]. However, other aspects of a female's behavior may affect her life-long fertility pattern, in that some females may consistently behave in ways to enhance their probability and frequency of producing offspring. For example,







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