

Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys?

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Abstract Invertebrates are the main source of protein for many small-to-medium sized monkeys. Prey vary in size, mobility, degree of protective covering, and use of the forest, i.e. canopy height, and whether they are exposed or embed themselves in substrates. Sex-differentiation in foraging patterns is well documented for some monkey species and recent studies find that color vision phenotype can also affect invertebrate foraging. Since vision phenotype is polymorphic and sex-linked in most New World monkeys - males have dichromatic vision and females have either dichromatic or trichromatic vision - this raises the possibility that sex differences are linked to visual ecology. We tested predicted sex differences for invertebrate foraging in white-faced capuchins *Cebus capucinus* and conducted 12 months of study on four free-ranging groups between January 2007 and September 2008. We found both sex and color vision effects. Sex: Males spent more time foraging for invertebrates on the ground. Females spent more time consuming embedded, colonial invertebrates, ate relatively more “soft” sedentary invertebrates, and devoted more of their activity budget to invertebrate foraging. Color Vision: Dichromatic monkeys had a higher capture efficiency of exposed invertebrates and spent less time visually foraging. Trichromats ate relatively more “hard” sedentary invertebrates. We conclude that some variation in invertebrate foraging reflects differences between the sexes that may be due to disparities in size, strength, reproductive demands or niche preferences. However, other intraspecific variation in invertebrate foraging that might be mistakenly attributed to sex differences actually reflects differences in color vision [*Current Zoology* 56 (3): 300–312, 2010].

Key words Male Foraging, Female Foraging, *Cebus*, Dichromacy, Trichromacy, Invertebrate Foraging

Intraspecific Variation in Foraging Patterns

Free-ranging animals face many decisions when selecting their diet and in meeting their nutritional requirements. They must choose where and when to forage, which foods to target and how they will obtain these foods once they are found. Considerable intraspecific variation in foraging patterns can be seen among individuals. Individual-level characteristics such as size, strength, dexterity, age, reproductive condition and previous experience lead to differences in metabolic rate, predation risk, and foraging efficiency, which in turn affect their foraging decisions. Gregarious animals have the added complication of coping with increased feeding competition imposed by conspecifics foraging in close proximity. Understanding the nature and extent of intraspecific foraging variation between individuals, and within social groups for gregarious species, has been a

long-standing goal of behavioral ecologists. The hope is to more accurately identify the selection pressures operating on individuals, and how they attempt to maximize their fitness through foraging decisions. Isolating the key variables affecting foraging decisions is difficult because many are correlated, such as age and experience, and size and strength. Previous efforts to understand individual variation in primate foraging have largely focused on sex differences, which are correlated with many of these key variables, especially in dimorphic species, and sex-linked patterns have proven to be powerful explanatory tools (Beck et al. 2007; Clark et al. 1998; Fragaszy and Boinski 1995; Ginnett and Dement 1997; Rabatsky and Waterman 2005).

In recent years, the adaptive nature of sex-linked color vision polymorphism possessed by New World monkeys has received much attention (Hiramatsu et al. 2008; Hiwatashi et al. 2009; Melin et al. 2009; Osorio et

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al. 2004; Riba-Hernandez et al. 2004; Rowe and Jacobs 2004; Smith et al. 2003; Stoner et al. 2005; Vogel et al. 2007; Vorobyev 2004; Yamashita et al. 2005) and there is growing evidence that color vision phenotype can also affect the foraging patterns and efficiencies of monkeys. Trichromatic color vision is advantageous for detecting or selecting yellowish to reddish food items against a green, leafy background (Osorio et al. 2004; Smith et al. 2003) or discriminating edible, ripe fruits (Melin et al. 2009; Sumner and Mollon 2000). Because chromatic contrasts are luminance-independent (Pokorny et al. 1991), trichromat advantage is expected to be most prevalent when luminance cues are unreliable, such as in forested environments where sunlight falling through vegetation creates dappled illumination (Mollon 1989). Alternatively, dichromacy may confer an advantage over trichromacy for breaking camouflage. The perception of hue can mask or delay the detection of boundaries between a target and background. In this way, random color variation can inhibit a trichromatic observer from seeing achromatic features, such as patterns, shapes and textures (Morgan et al. 1992). Because dichromats make fewer chromatic distinctions, they are less susceptible to color interference and may rely more heavily on achromatic (luminance) cues. Experimental studies using simulations of camouflage find that dichromatic humans (Morgan et al. 1992) and non-human primates (Saito et al. 2005) have an enhanced ability to detect color-camouflaged objects. In naturalistic foraging situations, this camouflage-breaking ability seems to help dichromatic monkeys detect cryptic prey, specifically palatable, exposed invertebrates, which are often color-camouflaged (Gullan and Cranston 2005; Lev-Yadun et al. 2004). Both captive and field studies on neotropical monkeys have found that dichromats capture more insects per foraging time than trichromats, especially under low-light conditions (Buchanan-Smith et al. 2005; Caine et al. 2009; Melin et al. 2007). Since color vision is sex-linked in these monkeys, this raises the possibility that their visual ecology may account for some well-known sex differences (de Ruiter 1986; Fedigan 1990; Fragaszy 1990; Fragaszy and Boinski 1995; Fragaszy et al. 2004; Fragaszy 1986; Robinson 1981; Rose 1994) in invertebrate foraging behaviors.

In this paper we test specific hypotheses concerning sex differences in foraging behavior. We chose capuchin monkeys as our study subjects because the color vision of this species is well understood (Hiramatsu et al. 2004; Hiramatsu et al. 2005; Hiwatashi et al. 2009; Melin et al. 2009), because they are highly insectivorous (Chapman

and Fedigan 1990; Fragaszy et al. 2004; Young 2005) and because sex differences in foraging have been well documented for these monkeys (Fragaszy 1990; Fragaszy and Boinski 1995; Fragaszy 1986; Rose 1994). We begin by providing a brief introduction to the nature of polymorphic color vision in capuchin monkeys. We then review some of the previously documented sex differences in their invertebrate foraging patterns and outline the testable predictions that arise from these studies. We hope that by identifying which, if any, sex differences in foraging can be linked to color vision phenotype, we will be better able to elucidate the selective pressures that operate on intraspecific variability in food search tasks and diet selection.

Polymorphic Color Vision in Cebus Monkeys

Like the majority of New World monkeys, excluding owl monkeys (Jacobs et al., 1993) and howler monkeys (Jacobs et al., 1996; Regan et al., 1998), capuchins possess a polymorphism of the opsin gene encoding for mid-to-long wavelength sensitive (M/LWS) photopigments (Hiramatsu et al. 2004; Hiramatsu et al. 2005; Jacobs and Blakeslee 1984; Mollon et al. 1984). Because this gene is located on the X-chromosome, heterozygous females are capable of trichromatic vision, whereas homozygous females and males, like the majority of mammals, have dichromatic vision, a condition commonly referred to as “red-green colorblindness.” There is interspecific variation in the number of opsin gene alleles, which ranges from two alleles, as seen in the case of spider monkeys, Genus *Ateles* (Hiramatsu et al. 2004) to five alleles, as in titi monkeys, Genus *Callicebus* (Jacobs and Deegan 2005). Capuchins have the most common number of alleles found among New World monkeys, three. This tri-allelic system predicts that, if alleles are present at equal frequencies, approximately two thirds of females will be trichromats and the rest will be dichromats.

Sex Differences in Invertebrate Foraging by Cebus Monkeys

Animal prey is the predominant source of protein for capuchin monkeys and it is of critical importance to these highly active and intelligent animals. Foraging behaviors that lead to the acquisition of animal matter should therefore be strongly affected by natural selection. The vast majority of prey items in the capuchin diet take the form of insects and other invertebrates

(Fragaszy et al. 2004) and differences between males and females are especially pronounced for invertebrate foraging patterns. That capuchins have a high proportion of invertebrates in their diet is not surprising given the densities and diversity of such potential food items - invertebrates in tropical forests come in a vast array of forms and sizes. They also possess a variety of defense strategies and can be found at different locations in the forest (Young 2005), which may make them more or less appealing to male and female monkeys as food items.

Several sex differences in invertebrate foraging have been previously reported. Males spend more time than females foraging on or near the ground, which is most often attributed to the lower predation risk they experience, given their larger body size (Fedigan 1990; Fragaszy et al. 2004; Rose 1994). Males have also been reported to consume animal prey, including invertebrates, more frequently than females, despite the fact that females spent proportionally and absolutely more time searching for prey (Fragaszy and Boinski 1995). Other studies also support the latter result and find that females spend more time than males engaged in foraging behaviors targeted at invertebrate animal prey (Fedigan, 1990). Fragaszy and Boinski (1995) have found significant differences between the sexes in how they foraged for invertebrate prey. Females did so more often than males by investigating dead wood and debris in palms, while males gleaned invertebrates from the surfaces of vegetation more often. There also appear to be sex differences in the types of invertebrates preferred by males and females. Males are reported to eat larger invertebrates (Rose 1994), more mobile prey (Fragaszy et al. 2004), and more snails, which require extensive processing by pounding on substrates or puncturing with canine teeth, prior to ingestion (Fragaszy 1986). Males are also described to be more efficient foragers, capturing more invertebrates per unit time (Fragaszy 1990; Fragaszy and Boinski 1995; Fragaszy 1986). Females have been reported to spend more time in extractive foraging and to eat more invertebrates that are embedded in substrates, such as branches and under bark (Fedigan 1993; Fragaszy 1986). It is not clear, from a biological point of view, why females seem to prefer embedded insects, since extractive foraging is often more strenuous and a bigger body size would be advantageous. Fragaszy and Boinsky (1995) emphasize that sources of variation between the sexes are not necessarily linked to body size or experience. It is possible that females prefer embedded invertebrates because they are

a more predictable and reliable resource (Fedigan 1993).

Three evolutionary explanations are commonly invoked to explain the above-listed sex differences in foraging behavior (Rose 1994): 1) Sexual dimorphism caused by intrasexual selection for larger body size in males; 2) Reproductive demands due to increased metabolic costs of lactation and pregnancy in females; and 3) Niche differentiation to avoid direct competition with mates and offspring. In this paper we explore a fourth possible explanation, that variation in color vision perception may make certain resources easier to locate and exploit, thereby affecting the costs and benefits of foraging for different food types and ultimately influencing foraging decisions. To test whether color vision phenotype can explain sex differences in invertebrate foraging by capuchin monkeys, we revisit predictions from previously published studies using our own data on free-ranging capuchins and test for independent sex differences and color vision differences. If color vision type explains sex differences, then we would expect to see differences between dichromatic and trichromatic females, but no difference between dichromatic females and males. If color vision does not affect sex differences, then we expect to see differences between males and dichromatic females, but not differences between dichromatic and trichromatic females.

Predictions Tested

Foraging Location

1. Males spend more time foraging for insects at or near ground level.

Time budget

2. Females devote a larger proportion of their activity budget to invertebrate foraging.
3. While foraging for insects, females devote a larger proportion of time to extractive behaviors whereas males devote a larger proportion of time to visual foraging.

Foraging Efficiency

4. Males are more efficient invertebrate foragers than are females (See methods for measure of foraging efficiency).

Invertebrate Diet Composition

5. Males eat more mobile prey.
6. Males eat more large prey.
7. Males eat more invertebrates that are protected by a hard shell.
8. Females eat more soft, invertebrates, lacking hard shells.
9. Females eat more embedded insects.

10. Males consume more invertebrate prey overall than do females.

1 Materials and Methods

1.1 Study site

We conducted our research in the Santa Rosa Sector of the *Área de Conservación Guanacaste* (ACG). This site lies in the Guanacaste province of Costa Rica, Central America. This area is highly seasonal for precipitation, temperature and humidity with the vast majority of the annual rainfall accumulating from mid-May through mid-December (Campos and Fedigan 2009; Fedigan and Jack 2001). The Santa Rosa Sector consists of Pacific lowland tropical dry forest. This area has been protected since 1970 and is in various stages of forest regeneration. Janzen (2002) provides a further description of this site.

1.2 Study species and subjects

White-faced capuchins are medium-sized, gregarious neotropical monkeys. They live in female philopatric social groups and are moderately sexually dimorphic; males are approximately 30% larger than females and are more robust, with longer canines (Masterson 1998; Rose 1994). Capuchins consume the fruit and flowers of a large variety of plant species (Fragaszy et al. 2004; Melin et al. 2008; Vogel 2005) and also rely heavily on animal prey. Vertebrate predation by capuchins is not uncommon (Fedigan 1990), however the majority of their animal prey is made up of insects and other invertebrates, which can account for 15%–45% of their overall diet (Chapman and Fedigan 1990; McCabe and Fedigan 2007; Young 2005). Capuchins are well known for the diversity of their invertebrate diet (Fragaszy et al. 2004; Melin et al. 2008; Rose 1994), and they are not easily dissuaded by prey defense mechanisms (Young 2005; Young et al. 2008).

We observed 4 social groups (“CP”, “EX”, “GN” and “LV”) of fully habituated white-faced capuchin monkeys, ranging in size from 8–35 members. Individuals were identified based on color and patterns in the fur, body size and, when present, scars, wounds or skin blotches. Because age is known to affect insect foraging patterns by capuchins (Fragaszy and Boinski 1995; Robinson 1981), for the current study, we included only those monkeys that were at least six years of age by the end of the study period. Individuals of this species are typically considered to be adults at this stage (Fedigan et al. 1996). Group composition and color vision typing for these individuals has previously been reported (Hiramatsu et al. 2005; Melin et al. 2009). In total, our

sample size consists of 49 monkeys: 19 dichromatic males, 13 dichromatic females and 17 trichromatic females.

1.3 Data collection

We collected behavioral data from January through May 2007, September 2007 through January 2008, and May through August 2008 for a total of 12 months, encompassing a full annual cycle. We performed 2–4 full-day follows (dawn to dusk, ~13 hours/day) per group each month, for a total of 1810 contact hours. We spent more time with the larger groups to obtain a relatively equal sampling effort among all study subjects. During contact hours, we conducted 10-minute focal animal follows (Altmann 1974) to record invertebrate capture events. For each capture, we recorded whether the monkey was visually foraging (scanning nearby substrates) or extractive foraging (picking at, biting, pulling on or sifting through bark, branches and leaves, or placing hands or feet inside holes or crevices). We also recorded the duration of time spent feeding on tiny invertebrates, which were too small to be recorded as individual capture events, such as wasp and termite larvae, as well as the duration of all visual and extractive behaviors. Additionally, on the hour and half-hour we conducted scan sampling (Altmann 1974) and recorded the location (ground, lower canopy, upper canopy) and behavior (foraging, resting, social or travelling) of all group members that we could locate within a 10-minute period. For foraging samples, we also recorded the type of foraging (extractive versus visual) and food type (invertebrate prey, vertebrate prey, fruit, flower or other). For the individuals included in this study, we collected 263 hours of focal animal data and 16,220 scan samples. We recorded data on hand-held PSION© Workabout computers using Behavior© software. Inter-observer reliability was evaluated throughout the study to ensure consistency among all researchers.

1.4 Invertebrate classification

We classified the invertebrates into five categories based on mobility, body size and degree of protective covering. A sixth category was created for invertebrates that we could not identify (Table 1). Invertebrates that were capable of fast movement (“mobile”) were considered large if monkeys required two or more bites to consume them, and small if they could be eaten in one bite. Mobile invertebrates included insects or arachnids, many of which had a carapace that was usually partially or entirely consumed (see Young 2005 for further detail). Stationary or slow-moving invertebrates (“sedentary”) were considered hard if they were protected by a tough

covering (shell or thick cocoon) from which the invertebrate was extracted prior to consumption. We considered them to be soft if they were unprotected by a tough covering. Larvae in thin cocoons were grouped with soft sedentary invertebrates as capuchins consumed the cocoon with the larva. Sedentary insects were not categorized by size; most were much smaller than the “large mobile” invertebrates. Capuchins also ate ant, wasp and termite larvae, as well as the adults, from thin branches, acacia thorns and wasp and termite nests. These “colonial” invertebrates were too small to be counted individually as they were being eaten. Colonial insects were only obtained through extractive foraging. Invertebrates in each of the other groups (mobile and sedentary) were captured by monkeys during both visual foraging and extractive foraging bouts.

1.5 Data analysis

We ran univariate ANCOVAs (analyses of covariance) in SPSS 16.0. In Table 2 we present the dependent and covariate variables for each of our analyses. We in-

cluded covariates to either a) control for our own sampling effort or b) to control for the effects of other variables. We measured foraging efficiency in two ways, depending on the size of the prey: a) when prey were large enough to be captured individually, we calculated the number of invertebrates captured per unit of time spent in foraging behavior, and b) when prey were too small and numerous to be counted as individual captures, we calculated the duration of time spent feeding on invertebrates per time spent foraging overall. For the foraging efficiency analyses, in addition to the total insects captured during visual foraging and extractive behaviors, we also broke down the capture rates by invertebrate type (large mobile, small mobile, hard sedentary and soft sedentary) to determine if monkeys are more or less efficient for specific types of invertebrates (not listed individually, i.e. by species, for brevity). Our predictor variable for each analysis was sex/color vision group: 1) dichromatic males, 2) dichromatic females, 3) trichromatic females. To test for specific sex or color vision

Table 1 Classification of invertebrates eaten by white-faced capuchins *Cebus capucinus* in Costa Rica

Type	Description	Examples: Common name (Order)
Large Mobile	Monkeys take 2 or more bites to ingest, ~3 cm in length or larger (up to ~10 cm).	Grasshoppers and katydids (Orthoptera), deadhead cockroaches (Blattaria), cicadas (Hemiptera), stick insects (Phasmida).
Small Mobile	Monkeys eat in 1 bite, ~ 1–2 cm in length.	Stink bugs (Hemiptera), beetles (Coleoptera), small cockroaches (Blattaria), small moths and butterflies (Lepidoptera).
Soft Sedentary	No protective exoskeleton, minimal processing required.	Non-spiny caterpillars, maggots and other insect larvae (ex. Hymenoptera), slugs (Stylommatophora).
Hard Sedentary	Hard, protective covering on invertebrate, removal required.	Snails (Stylommatophora), some heavily cocoon-bound larvae (Lepidoptera).
Colonial	Too small to be counted as individual captures, consumption recorded as duration.	Ants and wasps (Hymenoptera), termites (Isoptera).
Unknown	Invertebrate was not seen well enough to be classified.	

Table 2 Variables included in statistical analyses of invertebrate foraging (IF) by capuchin monkeys

	Analysis	Dependent Variable	Covariate
Foraging Location	Ground foraging time.	# IF scans at ground level.	Total # IF scans.
Time budget	Total invertebrate foraging time.	# IF scans.	Total scans recorded.
	Extractive invertebrate foraging time.	# Extractive IF scans.	Total # IF scans.
Foraging Efficiency	Efficiency for exposed invertebrates.	# Captured while visual foraging.	Duration visual.
	Efficiency for embedded invertebrates.	# Captured while extractive.	Duration extractive.
		Duration feeding colonial.	Duration extractive.
Invertebrate Diet Composition	Mobile invertebrates.	# Mobile captured.	Total captured.
	Large invertebrates.	# Large captured.	Total captured.
	Hard invertebrates.	# Hard sedentary captured.	Total captured.
	Soft invertebrates.	# Soft sedentary captured.	Total captured.
	Embedded invertebrates.	Total embedded captured.	Total captured.
		Duration feed embedded colonial.	Total obs. hours.
Total Invertebrates.	Total caught.	Total obs. hours.	

differences, we made two pairwise comparisons by comparing main effects (LSD) among the three groups using the estimated marginal means and the pairwise comparison output, which generates a mean difference (*MD*), standard error (*SE*) and a *p*-value. To test for the effect of sex, we compared males ($n = 19$) to dichromatic females ($n = 13$); and to test for the effect of color vision, we compared dichromatic females to trichromatic females ($n = 17$). Values reported in the results are the estimated marginal means \pm *SE*.

2 Results

2.1 Prediction 1: foraging location

We found a significant effect of color vision/sex group on foraging location. Pairwise comparisons revealed that males (8.88 ± 1.00) conducted a significantly higher ($MD = 6.815$, $SE = 1.518$, $P < 0.001$) number of invertebrate-foraging scans at ground level than did dichromatic females (2.07 ± 1.11). There was no significant difference between dichromatic females and trichromatic females. The mean of the covariate, total invertebrate-foraging scans recorded, was 121.00 scans (Fig. 1).

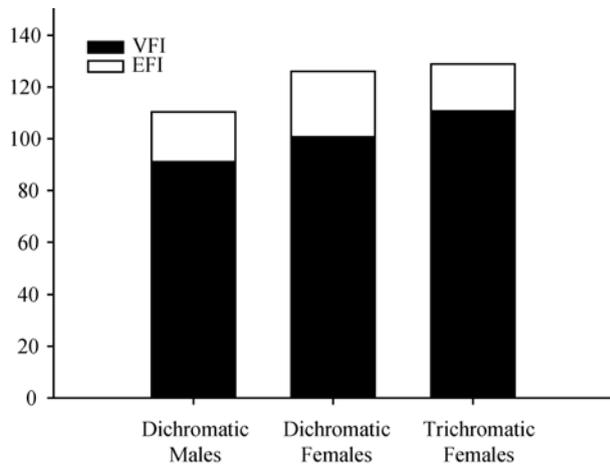


Fig. 1 Estimated marginal means of the number of scans in which dichromatic male, dichromatic female and trichromatic female capuchin monkeys were foraging for invertebrates at ground level

The covariate, total invertebrate-foraging scans recorded, is evaluated at 121.00. Scans have been separated into visual foraging for invertebrates (VFI) and extractive foraging for invertebrates (EFI).

2.2 Predictions 2 and 3: time budget

Color vision/ sex group had a significant effect on time spent foraging for invertebrates (Fig. 2). The mean of total scans was 331.02. Dichromatic females (126.11 ± 5.22) spent more scans foraging for invertebrates than males (111.02 ± 4.50) did, which was a significant effect

($MD = 15.083$, $SE = 6.896$, $P = 0.034$). We did not find a significant difference between dichromatic and trichromatic females for total invertebrate foraging time; however, we did find a significant difference ($MD = 8.765$, $SE = 3.576$, $P = 0.018$) in the time they devoted to different types (visual versus extractive) of insect foraging (Fig. 2). Of the total invertebrate-foraging scans recorded (mean = 121.02), trichromatic females spent more scans in visual foraging behaviors (105.73 ± 2.43) than dichromatic females (96.89 ± 2.59). Sex did not have a significant effect on time spent in extractive versus visual foraging behaviors.

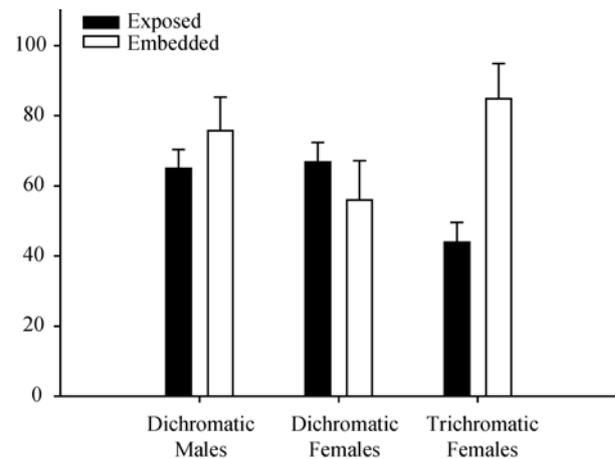


Fig. 2 Estimated marginal means of the number of scans in which dichromatic male, dichromatic female and trichromatic female capuchin monkeys were observed to be foraging for invertebrates

The covariate, total scans recorded, is evaluated at 331.02 scans. Scans have been separated into visual foraging for invertebrates (VFI) and extractive foraging for invertebrates (EFI).

2.3 Prediction 4: foraging efficiency

In total, we recorded 3496 capture events over the 12-month period of our study; of these, 647 were embedded insects captured via extractive behavior and 2849 were exposed insects captured during visual foraging. There was a significant color vision/sex effect on the number of exposed insects captured. Dichromatic females (66.79 ± 5.61) captured significantly more ($MD = 22.910$, $SE = 7.947$, $P = 0.006$) exposed invertebrates than did trichromats (43.88 ± 5.70), controlling for time spent in visual foraging (84.76 minutes). Furthermore, dichromatic females did not differ from males in capture efficiency of exposed insects, indicating there was no sex effect on capture rate (Fig. 3). During extractive foraging, trichromatic females captured the most embedded insects (15.21 ± 1.78), controlling for foraging duration (mean = 15.19 minutes; Fig. 3). Our pairwise

comparison of color vision types revealed a marginally significant difference between dichromatic (10.03 ± 2.02) and trichromatic females in capture rates during extractive foraging ($MD = 5.183$, $SE = 2.666$, $P = 0.058$).

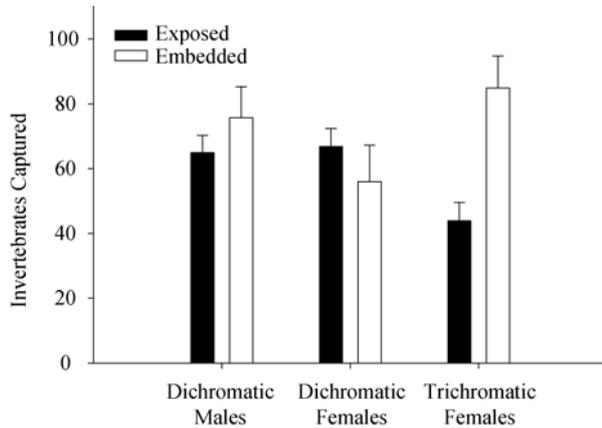


Fig. 3 Estimated marginal means of the number of exposed and embedded invertebrates captured by dichromatic male, dichromatic female and trichromatic female capuchins during visual foraging and extractive foraging, respectively

The covariate, total foraging, is evaluated at 84 minutes, which is the mean duration of visual foraging among subjects. Captures of embedded insects were extrapolated to match this foraging duration for comparison.

When we broke down efficiency of visual foraging by specific insect type (Fig. 4), we found significant sex differences in the capture rates of a) soft, sedentary ($MD = 8.922$, $SE = 3.796$, $P = 0.022$), b) hard sedentary ($MD = 1.276$, $SE = 0.349$, $P = 0.001$) and c) large mobile ($MD = 3.191$, $SE = 1.285$, $P = 0.017$) invertebrates. Males captured more large mobile invertebrates (7.07 ± 0.88) and hard sedentary invertebrates (1.56 ± 0.24), and fewer soft sedentary invertebrates (14.30 ± 2.58) than dichromatic females (3.88 ± 0.92 , 0.29 ± 0.25 , 23.23 ± 2.70 for large mobile, hard sedentary and soft sedentary invertebrates respectively; Figure 4). We also found one color vision effect: dichromats captured significantly more ($MD = 8.444$, $SE = 3.830$, $P = 0.033$) soft, sedentary insects than trichromats (14.78 ± 2.75) did. When we broke down extractive foraging efficiencies by insect type, we found one significant sex difference ($MD = 2.182$, $SE = 0.931$, $P = 0.024$): males (2.33 ± 0.60) caught more small, mobile insects than dichromatic females did (0.152 ± 0.70). All other comparisons were non-significant.

The analyses of colonial extractive foraging also revealed a significant sex difference ($MD = 2.569$, $SE =$

0.712 , $P = 0.001$). Females spent more time (5.07 ± 0.54 minutes) feeding on embedded, colonial invertebrates than did males (2.50 ± 0.46 minutes). There was no significant difference between dichromatic and trichromatic females in feeding on embedded colonial invertebrates. The covariate, duration of extractive foraging behavior, was evaluated at 15.19 minutes.

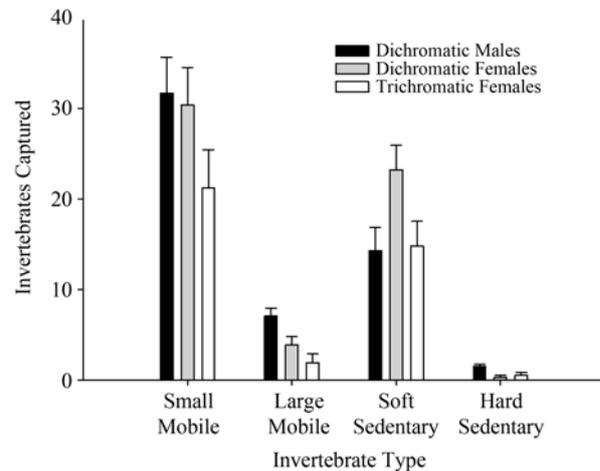


Fig. 4 Estimated marginal means of the number of small mobile, large mobile, soft sedentary and hard sedentary invertebrates captured by dichromatic male, dichromatic female and trichromatic female capuchin monkeys

The covariate, visual foraging duration, is evaluated at 84.76 minutes.

2.4 Predictions 5–10: invertebrate diet composition

Together, small and large mobile invertebrates made up approximately half (50%) of the prey captured by the monkeys over the course of this study. Of those, large invertebrates constituted ~10% of the total captured, with small invertebrates making up the other 40%. Sedentary invertebrates were also eaten frequently (~35%), although soft ones were consumed far more frequently (~33%) than hard ones (~2%). Unknown insects made up the final 15% of the total invertebrates captured. In Fig. 5 we present the mean number of invertebrates of each type captured by dichromatic males, dichromatic females and trichromatic females. The mean of the covariate was 71.35 total invertebrates captured.

We cannot directly compare the dietary importance of colonial versus individually captured invertebrates. Colonial invertebrates cannot be individually counted and we did not record a feeding duration for insects that were consumed in less than two bites, because monkeys continued foraging without noticeably stopping to consume their prey. However, similar information was measured for capuchins at the same study site for five months of the dry season and is available in Young (2005).

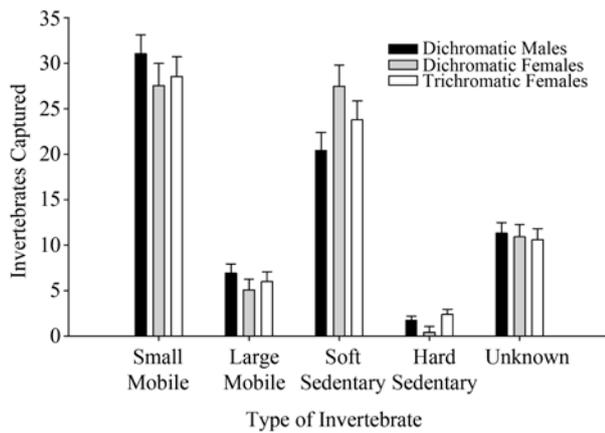


Fig. 5 Estimated marginal means of the number of small mobile, large mobile, soft sedentary, hard sedentary and unknown invertebrates captured by dichromat male, dichromat female and trichromat female capuchin monkeys

The covariate, total invertebrates captured, is evaluated at 71.35

Once we controlled for the total number of captures, we did not find a significant sex or color vision difference in the number of mobile invertebrates (small and large combined) captured or in the number of large invertebrates captured alone. We found variation in the numbers of hard sedentary invertebrates captured; males captured more (1.69 ± 0.52) than dichromat females (0.404 ± 0.61) and, unexpectedly, we found that trichromat females captured relatively more (2.39 ± 0.54) hard sedentary invertebrates than either males (1.69 ± 0.53) or dichromat females (0.40 ± 0.61). Only the color vision difference was statistically significant ($MD = 1.985$, $SE = 0.811$, $P = 0.018$). When examining foraging on soft sedentary insects, we found that dichromat females captured significantly more (27.45 ± 2.34) than males did (20.40 ± 2.00 ; $MD = 7.056$, $SE = 3.131$, $P = 0.029$). There was no significant difference between dichromat and trichromat females for the soft sedentary type (Fig. 5).

The capuchins caught far fewer embedded invertebrates (19%) than exposed invertebrates (81%) during our study. When we assessed the number of invertebrates captured from within a substrate (embedded) relative to total captures, we did not find a significant effect of sex or color vision. When we examined the duration of time spent feeding on colonial embedded insects, controlling for total observation time, we did find a significant sex effect ($MD = 2.995$, $SE = 0.856$, $P = 0.001$). Dichromat females spent more time feeding on colonial invertebrates (5.40 ± 0.64) than males (2.40 ± 0.57). Dichromat females also spent more time feeding on embedded colonial invertebrates than

trichromats (3.58 ± 0.60), but the difference between dichromat and trichromat females ($MD = 1.824$, $SE = 0.885$, $P = 0.045$) was less than the difference between females and males. In our final analyses, we asked whether males captured more invertebrates overall, controlling for observer sampling effort via hours of observational (obs.) time. We did not find an effect of sex on total invertebrates captured, nor did we find an effect of color vision phenotype for this measure.

3 Discussion

3.1 Foraging location

Our results on foraging location are in accordance with prediction 1 and with prior studies (de Ruiter 1986; Fedigan 1993; Fragaszy 1990; Fragaszy 1986; Robinson 1981; Rose 1994), which found that capuchins exhibit sex differences in time spent at different foraging locations. We found that male capuchins spent much more time foraging at ground level than either dichromat or trichromat females did. Sex differences in foraging location may be due to differences in body size between males and females. Male capuchins are 30% larger than females, which might a) lower their risk of being preyed upon and permit more time in “risky” foraging locations, such as on the ground (Boinski 1989; Chapman 1986; Cowlshaw and Dunbar 2000; Fragaszy et al. 2004; Miller 2002) or b) restrict their access to upper canopy locales, where the thinner branch supports may not be sufficient to support their body weight. Similar effects of body size on forest utilization have been reported interspecifically for sympatric monkeys (Fleagle and Mittermeier 1980) and intraspecifically for other sexually dimorphic mammals, such as didelphid marsupials (Cunha and Vieira 2002). However, sexual dimorphism in body size may only affect habitat use when the larger sex exceeds the capacity of the smallest, commonly used support structures (Loretto and Vieira 2008).

Rose (1994) found that time spent foraging at ground level was correlated with invertebrate capture efficiency by capuchins. Despite their differences in foraging location, we did not find a difference in the overall capture efficiency between males and dichromat females; however, we did find differences in efficiency for specific types of invertebrates. For example, males were more efficient at capturing large mobile insects, such as grasshoppers and crickets, which are often terrestrial and captured on the ground or within 5 meters of the ground (Rose 1994), whereas dichromat females were more efficient at capturing the arboreal, leaf-eating caterpillars (soft sedentary prey). Therefore, some differ-

ences in the time spent at different foraging location may reflect preference for and efficiency of obtaining prey found in different areas of the forest.

3.2 Time budget

Females devoted a larger proportion of their activity budget to insect foraging than did males. This is consistent with prediction 2 and with the results of Fragaszy and Boinski (1995), who found that female wedge-capped capuchins *C. olivaceus* spent more time foraging for animal prey, including invertebrates and with Fedigan (1990), who found that females spent more time foraging for invertebrate prey than males did, although males engaged in vertebrate predation more often than females. Sex differences in foraging effort among mammals are usually attributed to the increased reproductive demands of pregnancy and lactation in females (Lee 1987) and reproductive effects on the foraging of capuchins at our study site have previously been reported (McCabe and Fedigan 2007). Invertebrates are the main source of protein for frugivore-insectivore primates, like capuchins, versus, for example, frugivore-folivores such as woolly monkeys, who obtain protein from leafy matter and seeds (Peres 1994). The need to obtain protein in the form of insects (or other invertebrates) constrains the activity budgets (Terborgh 1983) of insectivorous animals. This appears to be especially true for female capuchins at our site, perhaps because they have smaller bodies and digestive tracks and require higher dietary protein than males (Demment 1983). This may also be exacerbated by sex-differentiated costs of reproduction (Herrera and Heymann 2004) although a previous study at this site did not find that reproductive females consumed higher amounts of protein (McCabe and Fedigan 2007)

We were also interested in further partitioning the insectivorous time budget among color vision/sex groups. When we controlled for time spent foraging for invertebrates, we did not find a sex difference for time spent in extractive versus visual foraging behaviors, which is contrary to prediction 3 in that we expected females to spend more time in extractive foraging behaviors and males to spend more time in visual foraging (Fragaszy 1990; Fragaszy and Boinski 1995; Fragaszy et al. 2004; Fragaszy 1986). What we found instead was a difference attributable to color vision phenotype: trichromatic females spent relatively more time visually foraging and less time extractively foraging than dichromatic females or males. This pattern was seen in a previous study (Melin et al. 2008), but this is the first time a statistically significant effect has been found.

Increased time spent visually foraging by trichromats could relate to their reduced foraging efficiency in capturing exposed insects, which we discuss further in the following section. We were surprised that trichromats did not spend more time in extractive behaviors than dichromats, given their higher efficiency. Perhaps the time available for extractive foraging is limited, given that extractive behaviors are stationary and groups of capuchins usually move frequently and travel long distances over the course of a day (Campos and Fedigan 2009).

3.3 Foraging efficiency

Contrary to prediction 4, males were not more efficient than females at capturing invertebrate prey. We found that males and dichromatic females were equally efficient at capturing exposed invertebrates, and that both exceeded the ability of trichromatic females to capture exposed invertebrates. We interpret this result as a dichromatic advantage in breaking the crypsis of exposed invertebrate prey. Because trichromats are expected to be more susceptible to color-camouflage, and consequently to have lower foraging efficiency for cryptic foods, it is possible that previous studies finding a sex difference in foraging efficiency were confounded by the color vision phenotype of their subjects. Females may have been performing less well as a group due to the presence of trichromats, which the majority of females are, given the tri-allelic nature of color vision polymorphism in capuchins (Hiramatsu et al. 2005; Jacobs 1993; Jacobs 1997). However, we did note differences in foraging efficiencies for some invertebrate types. Males were more efficient at capturing large mobile and hard sedentary invertebrates, whereas females were more efficient at capturing soft-sedentary insects, predominantly caterpillars. This finding may be attributable to preferences of each sex in foraging location, although measures of invertebrate densities at different forest heights would be needed to verify this. This effect may also be due to members of each sex targeting different invertebrate types. This is difficult to measure in the wild, but invertebrate preferences could be tested in a captive or controlled situation.

An effect of color vision type was detected when we examined extractive foraging efficiencies. Trichromatic females in this study had the highest capture rate of individually-caught embedded prey, a result that is consistent with previous studies at this site (Melin et al. 2007). Only when we considered the colonial-type prey did we find a sex difference: females spent more time feeding on these invertebrates (ants, wasps, termites and

their eggs/ larvae) than males did, when controlling for duration of extractive behaviors. This can be viewed as increased foraging efficiency for this food type and may be a result of females devoting more of their extractive foraging effort to locating colonial invertebrates. We did not subdivide extractive behaviors into “strenuous” versus “quiet” types, as has been done elsewhere (Fragaszy 1990; Fragaszy and Boinski 1995; Fragaszy 1986). This type of categorization may reveal further sex differences in extractive foraging behaviors and shed more light onto this subject in future studies.

3.4 Invertebrate Diet Composition

Our data supports two of the six predictions we tested regarding the composition of capuchins' invertebrate diet: 1) Females ate more of the soft, sedentary-type of invertebrates than did males (prediction 8) and 2) females ate more embedded invertebrates than did males, although this was limited to the colonial variety (prediction 9). Interestingly, females were also more efficient at foraging for these two invertebrate types. These results support previous reports of females specializing on “reliable” prey sources that are unlikely to escape once located (Fedigan 1990; Fragaszy et al. 2004). These findings may also reflect females' preferences for softer food types, like caterpillars and grubs, which are easier for individuals with smaller teeth and jaw musculature to consume than mobile insects with tougher exoskeletons or snails with shells that are extremely hard to crack through.

In previous studies, male capuchins have been reported to eat more mobile prey (Fragaszy et al. 2004), prediction 5, more large prey (Rose 1994), prediction 6, and more snails or other prey enclosed in hard protective coverings (Fragaszy and Boinski 1995), prediction 7, than females. In our study, males and females did not differ in foraging efficiency for small, mobile prey, which made up the vast majority of all mobile prey captures, so it is not surprising that we did not find a sex difference in dietary composition of mobile prey. However, we did find that males were more efficient foragers for large mobile and hard sedentary invertebrate types, but that they did not eat relatively more of them than females. Given these variations in foraging efficiency between the sexes, this result is surprising. There are several possible explanations. As snails and large invertebrates made up only 2% and 9% respectively of the invertebrate diet, larger sample sizes may reveal a significant difference. Fragaszy and Boinski (1995) found that males ate more snails than females; however, at their site, snails constituted 40% of the invertebrate diet.

Snails at their site may also have been larger than those found in Santa Rosa, making larger canines and stronger jaws relatively more important. The category of “unknown” invertebrates, which made up 15% of the diet in our study, may also be absorbing some of the variation. And finally, seasonal differences in invertebrate diet may be present. Rose's (1994) study took place predominantly during the dry season (January – May), when large invertebrates are more frequently eaten (Melin, unpublished data). Our study occurred over an annual cycle, which may have diluted some of the dietary divergence between males and females, if it is stronger during the dry season. Seasonal effect on diet divergence would be a promising area for future research, especially at highly seasonal sites such as Santa Rosa.

Our final analyses concern whether males ate more invertebrate prey overall than did females (prediction 10). We did not find a sex difference in total invertebrates captured, which is unsurprising given that males and females had similar capture efficiencies. We also did not find a color vision effect, even though dichromats captured more exposed insects, which made up over 80% of the insectivorous diet, than trichromats did. The most plausible explanations for this are that trichromats captured more embedded invertebrates than dichromats did, and also that trichromats increased their foraging effort for exposed insects by spending more time searching for them. As a final comment on this subject, it is worth noting that we found that females spent more time feeding on colonial invertebrates and do not differ from males regarding the number of individually-captured invertebrates. This may suggest that females had a higher overall invertebrate, and therefore protein, intake. However, a more detailed study that considers the nutritional content of each invertebrate type is warranted to investigate this.

3.5 Conclusions

The following sex differences found in invertebrate foraging patterns cannot be attributed to the differing color vision of males and the majority of females: 1) Time spent foraging on the ground; 2) Proportion of activity budget spent foraging for insects; 3) Time spent on and efficiency of consuming embedded, colonial invertebrates; 4) Proportion of soft sedentary invertebrates in diet. Rather, these variables must be affected by non-sensory attributes of sex, such as size, strength, predation risk or metabolic rate. Color vision phenotype does, however, affect the invertebrate foraging patterns of capuchin monkeys in other ways: 1) Increased cap-

ture efficiency of exposed insects by males is best attributed to their vision phenotype since dichromatic females are equally good at this task; 2) Trichromatic females spend more time visually foraging than do dichromatic females or males, perhaps to compensate for their reduced efficiency in foraging for exposed invertebrates.

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