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Specialized for the Reach: Visual Control of Fruit Picking and Positional Behavior Favor a Reach Over a Grasp Phenotype for Geoffroy's Spider Monkey (*Ateles geoffroyi*)

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Abstract – The Geoffroy's spider monkey (*Ateles geoffroyi*) has distinctive features, including a vestigial external thumb, elongated fingers and forelimbs, and a prehensile tail. The purpose of the present study was to understand how this derived morphology influences visually mediated reach and grasp movements during fruit picking. Wild spider monkeys, habituated to human observers, were filmed in Sector Santa Rosa (SSR), Área de Conservación Guanacaste in northwestern Costa Rica. We analyzed frame-by-frame video recordings of the monkeys picking 14 fruit species. The most frequent reach strategy was a branch-withdraw (62%; 1,338 of 2,164 fruit items), in which the monkeys hooked their fingers around a branch and pulled it toward themselves, to take the attached fruit by mouth. They sometimes used just their mouth to reach (17% of observations). Reaching with arm and hand extension to pick fruit by hand (21% of observations) was achieved using power grasps that relied on tactile cues. It is likely that picking fruit by hand or mouth involved foveal vision whereas grasping and manipulation branches used peripheral vision. Most fruit-picking sequences featured tail prehension on a branch, which extended the monkeys' reach horizontally and ventrally into the small distal branches of the canopy. The observed reach strategies and the configuration of visually guided reaching skills of the hands and mouth—contrasted with the absence of visually mediated grasps—indicate that spider monkeys exhibit a reach phenotype. This contrasts with the grasp phenotype of the sympatric capuchin monkey, which uses the thumb and fingers to pick individual fruit items. These findings support the idea that the reach and the grasp have separate evolutionary histories in spider and capuchin monkeys, potentially facilitating fruit harvesting in different microcanopy locations and thereby contributing to niche partitioning.

Keywords – Dual visuomotor theory, Niche partitioning, Visual reaching phenotype, Spider monkey reaching, Tail prehension feeding

> "*Spider monkeys cast a distinct morphological silhouette – long scrawny arms and a snaky prehensile tail arching from a narrow pot-belly torso, topped by a small round head and blunt face. The commitment of this relatively large-bodied platyrrhine to a large-tree, upper canopy milieu and to ripe fruit foraging is seen throughout its skeletal and craniodental morphology.*" Rosenbert et al (2008)

The visual control of skilled hand use has long been of interest to evolutionary biologists and psychologists, who study the evolution of skilled hand use in humans and its cognitive implications. One approach to understanding variations in skilled hand use—such as those employed for eating by humans—is dual visuomotor theory (Grant & Conway, 2019; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Karl & Whishaw, 2013; Knecht, 2000; Marzke, 1971; Nashner et al., 1985; Sartori et al., 2015; Whishaw et al., 2019, 2025). This theory, supported by experiments that dissociate the visuomotor process of reaching and grasping, posits that the act of reaching for a target is directed by different classes of cues, including intrinsic (e.g., shape, size) vs extrinsic (e.g., spatial) cues. Movements directed by intrinsic cues include preshaping of the hand and fingers in anticipation of the grasp, the use of a precision grip in which the object is held between the distal pads of the thumb and fingers, and foveal gaze to identify grasp and bite points. Movements guided by extrinsic cues bring the hand to the target's location and may involve whole-hand grasps, the use of nonfoveal vision, and reliance on tactile feedback. A reach phenotype would involve reaching associated with whole-hand or power grasps, whereas a grasp phenotype would involve reaching that culminates in the use of the distal thumb and digits for precision grasps (Napier, 1956, 1962).

The modular structure of reaching has led to the suggestion that the reaching and grasping components of movement may have separate evolutionary histories (Karl & Whishaw, 2013; Whishaw & Karl, 2014, 2019). Comparative study of visual control of reaching in nonhuman primates provides evidence for phylogenetically related variation from which such histories may be inferred. Strepsirrhines, an early-branching primate suborder, display a reach strategy when grasping or holding food (Peckre et al., 2019, 2023). By contrast, catarrhine primates such as macaques (*Macaca*) display a grasp strategy (Hirsche et al., 2022; Macfarlane & Graziano, 2009; Marzke et al., 2015; Pouydebat et al., 2008; Scott, 2019). Among platyrrhine primates, capuchins excel in elements of a grasp strategy but do not display true precision grasps involving thumb–finger pad opposition as seen in catarrhine primates (Christel, 1993; Christel & Fragaszy, 2000; Whishaw et al., 2024a, 2024b; Truppa et al., 2019). The present study was undertaken to contribute to the comparative understanding of platyrrhine reaching by examining the natural foraging of the spider monkey—a sympatric of the capuchin monkey that also forages for fruit in the upper tree canopy.

The spider monkey (*Ateles* spp.) is a large platyrrhine primate found across Mexico, Central America, and South America (Mittermeier & van Roosmalen, 1981; van Roosmalen, 1985; Youlatos, 2002, 2008). *Ateles* are considered ripe-fruit specialists, and the diet of *Ateles geoffroyi* consists of approximately 80% fruit from as many as 364 plant species (González-Zamora et al., 2009; Scherbaum & Estrada, 2013). They prefer the softest ripe fruit, the seeds of which are defecated, aiding the dispersal and regeneration of fruiting trees (Link & Di Fiore, 2006; Stevenson et al., 2002; Whitworth et al., 2019). They occasionally eat leaves, flowers, and slow-moving insects (Link, 2003). Their distinctive morphological features—including a vestigial thumb, prehensile tail, limb joint hypermobility, prehensile lips, large spatulate incisors, and non-serrated molars—have invited several functional explanations (Cant, 1986; Jenkins et al., 1978; Jungers & Stern, 1981; Mittermeier & van Roosmalen, 1981; Melin et al., 2022; van Roosmalen, 1985; Riba-Hernández et al., 2003; Saint-Hilaire, 1806; Tague, 1997; Youlatos, 2002, 2008). For example, the locomotion theory (Cant, 1986; Strier, 1992; Rosenberger, 1992; Youlatos, 2008) proposes that brachiation, with tail-assisted support, facilitates movement through a patchily distributed fruit-tree habitat. Of relevance to the present study, the diet theory (Rosenberger et al., 2008) proposes that acquiring ripe fruit located in the fine branches of the upper canopy has been central to their morphological specialization. Other reasons for studying natural fruit foraging in spider monkeys include complementing laboratory-based studies of platyrrhine hand use (Christel & Fragaszy, 2000; Costello & Fragaszy, 1988; Nelson, 2024; Spinozzi et al., 2004; Truppa et al., 2019, 2021). Additionally, laboratory studies of laterality in primates (MacNeilage, 1987) have yielded mixed results for spider monkeys (Boulinguez-Ambroise, 2022; Caspar, 2022; Hook-Costigan et al., 1996; Motes Rodrigo et al., 2018; Nelson et al., 2015a, 2015b), which a study of handedness in natural foraging may help clarify. The neural systems of spider monkeys have been relatively neglected in comparison with other primates (Chang & Ruch, 1947; Chico-Ponce de León et al., 2009; Lassek, 1943; Pubols & Pubols, 1972), even though they are described as large-brained primates, a trait shared with other frugivores (DeCasien et al., 2017; Milton, 1993). Although capuchin monkeys feature skilled hand use and possess direct corticospinal projections to motor neurons—projections facilitating grasping and largely absent in platyrrhine squirrel monkeys (Bortoff & Strick, 1993; Strick et al., 2021)—the presence and role of such projections in spider monkeys remains unknown. Thus, due to their close relationship to these sympatric species and their distinctive morphology, studying the visual control of hand use in natural foraging by spider monkeys may offer insights into the evolution of visually guided hand use and the organization of the nervous system of platyrrhine primates.

Methods

Ethics Statement

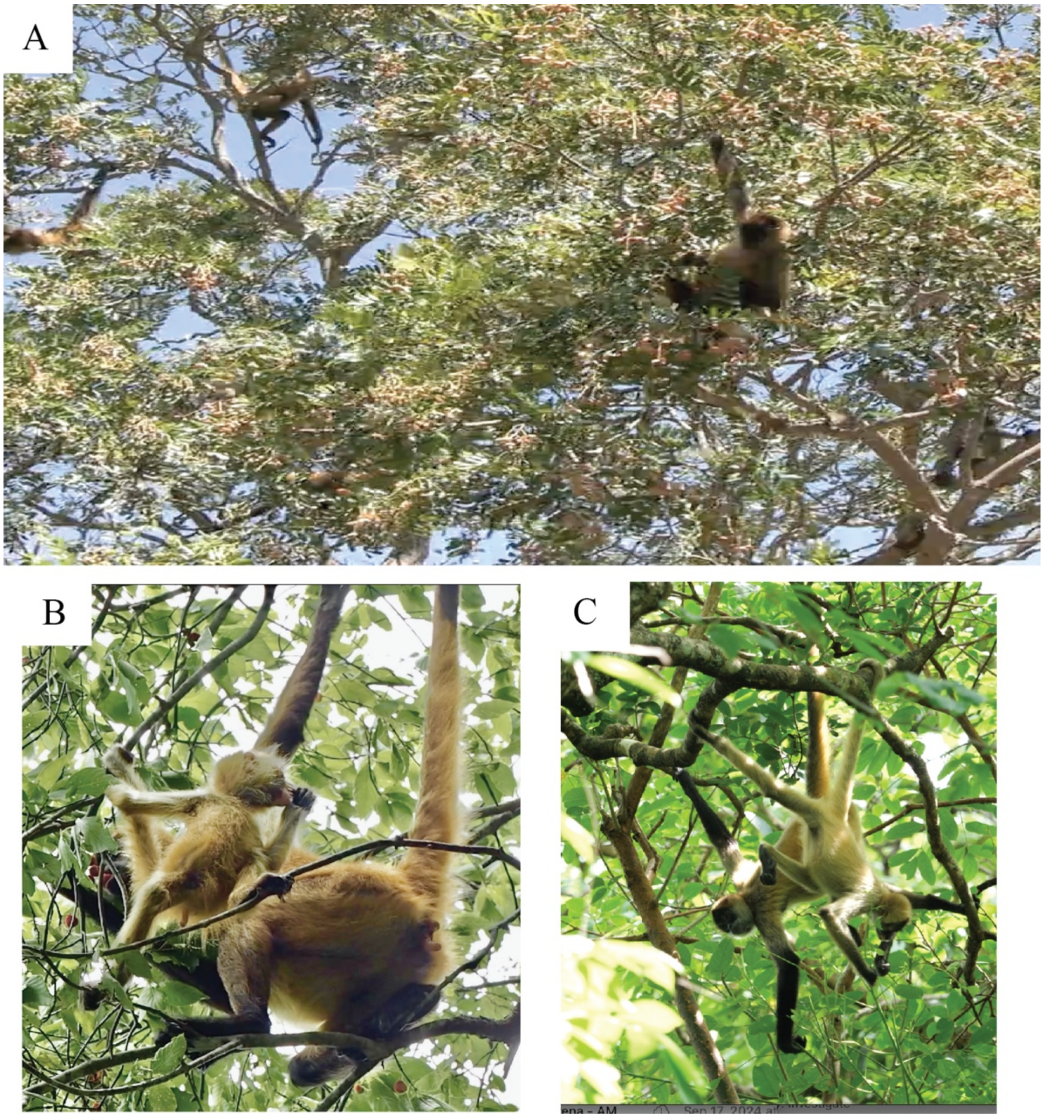
This research adhered to the laws of Costa Rica, the United States, and Canada and complied with protocols approved by the Área de Conservación Guanacaste (R-SINAC-ACG-PI-027-18) (R-025-2014-OT-CONAGEBIO), by the Canada Research Council for Animal Care through the University of Calgary's Life and Environmental Care Committee (AC19-0167).

Study Population

The feeding behavior of *Ateles geoffroyi* (Figure 1) was filmed in the Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10.836°, -85.615°). The habitat is a seasonal tropical dry forest, where long-term study of spider monkeys has been ongoing, described in detail elsewhere (Asensio et al 2012; Melin et al 2020). The age and sex distribution of 34 Geoffroyi's spider monkeys at filming were adult female (n=13), adult male (n=2), infant female (n=1), juvenile female (n=1), juvenile male (n=8), subadult female (n=6) and subadult male (n=4). Videos were obtained from one animal as a subadult female and later as an adult female. Thirty of the spider monkeys were individually identified and 4 were not identified from the film clips. The animals appeared to be in good health and featured no disabilities that interfered with climbing, food grasping or other aspects of feeding. Filming consisted of short (7sec–10 min) continuous video samples following a published protocol with strict out-of-sight rules, such that recording was done standing on the ground, typically between 5-20m from the study subject. We only recorded feeding behaviour when we had a relatively unobstructed view of the focal monkey (Melin et al., 2022). Individuals were sampled opportunistically, based on visibility, but distribution of the observations among sex and age classes were generally representative of the population. Each film clip was labeled with the monkey's ID for the purpose of identification.

Figure 1

Spider Monkeys (Ateles geoffroyi) Foraging



Note. A. Hungria, an adult female, foraging on the distal branches of a *Simarouba glauca* fruit tree. B. Inverness, an adult female with an infant, foraging in the branches of a *Guettarda macrosperma* tree. C. Inverness (background) with offspring, now a subadult (foreground) foraging on the leaves of a *Guettarda macrosperma* tree.

Video Recording

Video recording at 30 frames per sec (fps) provided *ad libitum* recordings of natural eating behavior and were collected using Lumix DC-G9, Sony FDR-AX53, and Olympus OM-D E-M1 camcorders.

Food Items

Spider monkeys were filmed eating fruits of fourteen plant species: *Doliocarpus dentatus* (ripe fruit diameter: 4 cm), *Bursera simaruba* (1 cm), *Coccoloba guanacastensis* (1 cm), *Dipterodendrum costaricensis* (2 cm), *Fictus ovalis* (1.5 cm), *Sciadodendron excelsum* (1.3 cm), *Karwinskia calderonii* (1.3 cm), *Guettarda macrosperma* (2.5 cm), *Ficus unknown* (3 cm), *Simarouba glauca* (1 cm), *Ficus cotinifolia* (1 cm), *Guazuma ulmifolia* (3 cm), *Spondias mombin* (4 cm), and *Bromelia plumieri* (6 cm). Fruit sizes are estimated to the nearest 0.5cm by experienced field researchers.

Video Analysis

We analyzed 134 video clips, which together comprised 4.48 hr of video. Each video clip provided an average of 16 examples of reaching for food items or for branches containing food items. Video recordings of spider monkeys were examined frame-by-frame using Quicktime 7.7 and Adobe Premier Pro software on an Apple computer by two observers (IQW and JD). Videos were scored using previously described methods (Hirsche et al., 2022; Peckre et al., 2023; Whishaw et al, 2024) and yielded an inter-scorer reliability coefficient of 0.96, based upon randomly selected videos representing approximately 10% of video cuts (Hallgren, 2012). Repeated scoring of the videos described visually mediated feeding sequences in which a spider monkey reached for, used a hand or mouth to grasp, or withdrew a food item to placed it into the mouth. Because animals were reaching through leaves and branches and adjusting posture, some component movements of some reaches were visible at times and others were obscured. The observable components were always scored.

Behavioral Analysis

Positional Behavior

The scoring of spider monkey positional behavior; i.e., posture and movement, is complicated by the many possible configurations of the limbs and tail (Cant, 1986). Here, as is shown in Figure 2, body position was scored on an 8-point scale (following Laird et al., 2022; Peckre et al., 2023) using an Eshkol-Wachman numeric-derived system (Golani, 1994; Whishaw et al. 2024); e.g., for a horizontal back orientation: “0”, hanging straight down with vertical torso “2”, inverted (i.e., torso horizontal with belly facing up) “4”, and upright with vertical torso “6”. Three aspects of behavior were scored:

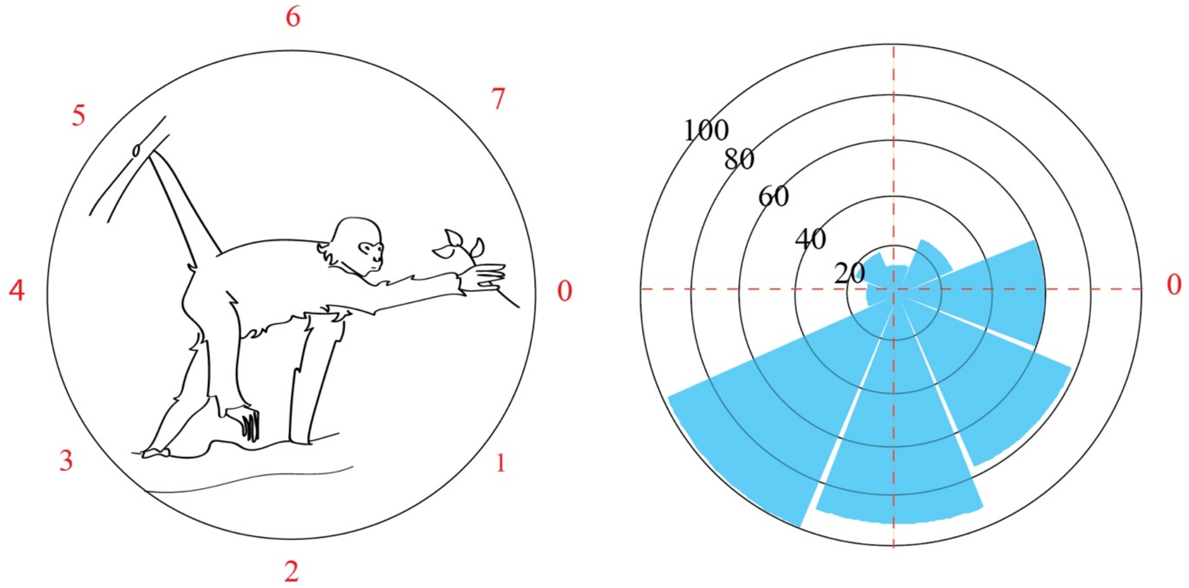
1. *Grasping*. An animal received a positional score at the point that it grasped a food item whether by hand or mouth.
2. *Consumption*. An animal received a positional score at the point that the food item was taken by the mouth directly or from the hand.
3. *Tail support*. Tail support was scored as “1” if it was judged that the monkey would fall if tail support was lost. If positional behavior did not depend upon tail support a score of “0” was given.

Figure 2

Positional Behavior and Tail Use for Grasping and Eating Fruit by Spider Monkeys

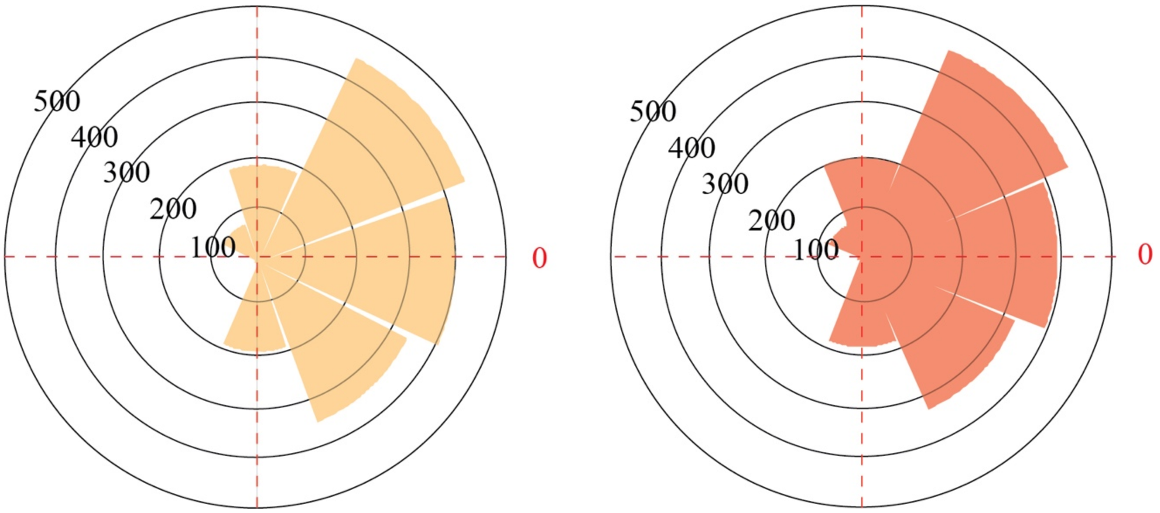
A. Vertical plane (score)

C. Tail prehension (percent)



B. Food grasp (number)

D. Food bite (number)



Note. A. Scoring system (from 0-7) for positional behavior that scores the long axis of the body in deviations of 45°; e.g., from a horizontal back orientation, illustrated for a monkey's "0" positional score in A. Hanging straight down with vertical torso = "2". Inverted (i.e., torso horizontal with belly facing up) = "4". Upright with vertical torso = "6". B. Percent of body positions used by spider monkeys that depended on tail support during reaching for a food item. C. The number of times spider monkeys adopted a body position as they reached for a fruit item. D. The number of times a spider monkey adopted a body position as they placed a fruit item in the mouth. The correlation between the body position used while reaching for fruit and the body position used while subsequently placing fruit in the mouth was Pearson r. =.940, *p* < .001, indicating that posture did not change between grasping (C) and placing fruit in the mouth (D).

Food-Purchase Movement

Four types of reaching and laterality were documented by counts:

Grasp-withdraw. A grasp-withdraw reach involved a single hand advancing to grasp a food item from a branch to bring it to the mouth.

Branch-withdraw. A branch-withdraw reach involved grasping a branch that was then brought toward the mouth so that a fruit item could be taken from the branch with the mouth or with a hand to be placed in the mouth.

Mouth-withdraw. A mouth-withdraw reach involved the mouth taking fruit items without the involvement of the hands.

Inhand-withdraw. An inhand-withdraw involved a food item already held in the hand being brought to the mouth.

Hand laterality. Use of the left or the right hand for each of the above four reach/withdraw types were counted to determine individual and population hand asymmetry (Hook-Costigan and Rogers, 1996; Motes Rodrigo et al., 2018; Nelson et al., 2015).

Hand Grasps

Hand grasps were described using Napier's (1956; 1962) classification and recent descriptions of capuchin monkey grasping (Whishaw et al, 2024a,b).

Precision grasp. A precision grasp involved holding an item between the distal thumb (digit 1) pad and one or more of the distal finger pads.

Power grasp. A power grasp involved clamping an item between the fingers (digits 2-5) and the hand palm, with no direct use of the thumb for holding.

Precision-power grasp. A precision-power grasp involved holding an item between the tip of one or more digits and the palm (Whishaw et al, 2024a,b).

Mouth Handling

The way in which the mouth grasped food items from the hand and then processed them was documented with counts of occurrences (Hirsche et al., 2022):

Incisor grasp. An incisor grasp involved the mouth opening and grasping a food item with the incisor teeth.

Premolar grasp. A premolar grasp involved the mouth opening and grasping a food item with the premolar teeth.

Chewing. Repeated mouth movements occurring following taking a food item by mouth were scored as chewing.

Spitting. If upon chewing a fruit item the monkey expelled some part of the fruit from its mouth, the act was scored as spitting.

Fruit sucking. If a monkey grasped a fruit item by mouth and chewed it without picking it from the stem, the act was scored as fruit sucking.

Component Movements of Reaching

Head Movement

The contribution of head movement to a withdraw-to-eat in reaching for a food item was scored on a 5-point scale (Hirsche et al., 2022; Peckre et al., 2023):

Score 0. The head was advanced toward the food item, and the food item was grasped with the mouth.

Score 1. The nose was placed near the food item, but the item was grasped by hand and brought to the mouth by hand.

Score 2. The hand holding the food item and the mouth were brought toward each other such that the withdraw-to-eat movement was accomplished equally by the hand and mouth.

Score 3. Most of the withdraw-to-eat was accomplished with the hand holding the food item with only a small orienting movement made by the mouth toward the hand.

Score 4. The head was not advanced toward the food item, or even withdrew, as the hand brought the fruit toward the mouth.

Hand Rotation

The following hand rotation movements were scored:

Pronation. A hand movement that involved hand rotation such that the palm faced downward was designated as pronation.

Supination. A hand movement that involved hand rotation such that the palm faced upward was designated a supination.

Movement Kinematics

Kinematic analyses of arm, hand, and eye movements were conducted using the open access software program Tracker (https://physlets.org/tracker/). Event times and body, hand and eye coordinates were manually marked frame-by-frame for the duration of a reaching for fruit act. Coodinates (x,y) were transferred from Tracker to Microsoft Excel (https://www.microsoft.com/en-ca/microsoft-365/mac/microsoft-365-for-mac) to generate graphical representations as movement velocity. Figures were made in Adobe Illustrator (https://www.adobe.com/ca/products/illustrator.html).

Statistical Analyses

Each fruit retrieval act was counted in terms of the acting animal, fruit type, positional behavior, and retrieval type. Posture, hand grasping type, eye engage and disengage, blinking and eye gaze direction are counted and reported as total number observations per fruit retrieval act. Conjunctions of behaviors were assessed using the Pearson product-moment correlation and compared with Chi-square tests. Group comparisons (e.g., position behavior, reach type, etc.) that featured sex (male, female) and age (juvenile, adult) were made using a generalized linear model repeated measure analysis of variance using SPSS (29.0.1.1) that designated probability and power. Follow up tests were Newman-Keuls. Laterality measures were made using Student's t-tests with the comparison variable being chance occurrence. The temporal relationships between movements are described kinematically. Statistical values of $p < .5$ were considered significant (Cote et al., 2021).

Results

General Foraging Observations

Video footage demonstrated spider monkeys are highly adept in moving through the trees, including the distal branches of trees (Figure 1). Feeding principally occurred in the canopy, in which the monkeys harvested fruit from the terminal canopy branches. The spider monkeys displayed a rich array of positional behavior and food purchase strategies to access food on every location on a tree. Given that the data were obtained from the spontaneous behavior of the animals in trees, the movements of reaching were associated with the movement of the animals themselves, the movements of the branches produced by the animal's positional changes, the wind, and movements of other animals. Behavioral observations were scored despite the complexity of substrate and positional movements. There were some occurrences of reaching acts associated with bringing a food item to the nose for sniffing, grasping a food item and not picking it, and grasping fruit that was then dropped (Melin et al., 20129), but these were not counted.

Positional Behavior and Prehensile Tail Use

Figure 2 (Video 1) summarizes positional behavior and the corresponding use of the tail in grasping branches for support. Figure 2A illustrates the scheme for the numerical scoring (0-7) for position based on the long axis of the body.

Figure 2B illustrates the percentage of positions in which a spider monkey depended upon tail support when grasping a food item. In all, 770 of 1597 (48 %) of reaches were dependent on tail support. The use of tail support in relation to posture was similar across all animals, as indicated by a repeated measures ANOVA that gave a significant group position effect, F(7,210) = 2.36, p = .024, n^2= .79, power = 1, with no significant difference in tail use in adults vs juveniles/subadults, F(1,30) = 0.78, p = .78, n^2= .32, power =.45 or males vs females, F(1,30) = .63, p = .43, n^2= .26, power = .47.

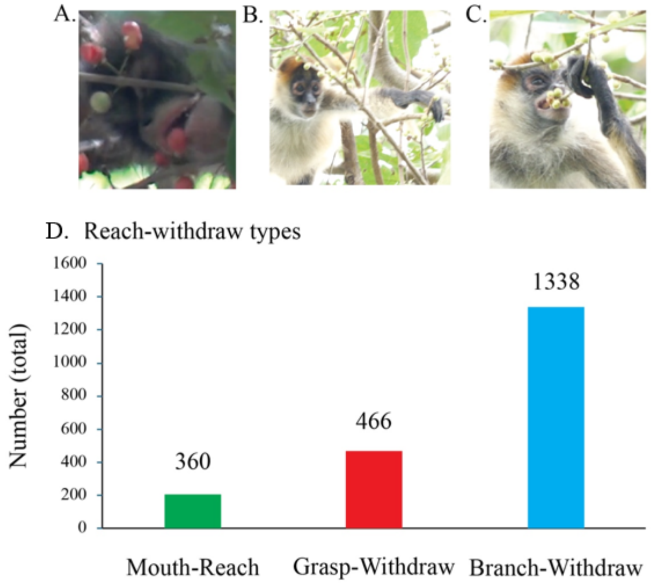
Figure 2C illustrates the distribution of the number of positions adopted by the spider monkeys as they grasped 1,597 fruit items. A repeated measures ANOVA gave a significant group effect of position, F(7,210)=11.2, $p < .001$, n^2=.,27, power =.1, in which sit, horizontal, and inclined were the most frequently used positions. There was no significant difference in the distributions of positions adopted by adult vs subadult/juvenile animals, F(1,30) = 1.07, p = .32, n^2 = .03, power = .17, or males vs females, F(1,30) = .26, p = .62, n^2=.01, power = .08. The correlation between the position used when grasping and the position used when placing the fruit in the mouth was highly significant (Pearson r = .940, $p < .001$). Thus, there was little adjustment in an animal's position between picking a fruit item and then placing it in the mouth (Figure 2C - 2D).

Mouth-Withdraw

Mouth-withdraw movements (Video 2) were used for taking all species of fruits. There was no correlation between fruit size and the incidence of mouth-withdraw movements (Pearson correlation, r = .320, F(1,14) = 1.3, p = .270. Nevertheless, some fruit species were preferentially taken directly by mouth. The highest incidence was associated with picking the fruit *Sciadodendron excelsum,* which grows in upward facing clusters on relatively large branches. The only strategy observed for taking this fruit was with the mouth, usually from a position with the head located above the fruit cluster (18.5% of all mouth withdraw observations). The second highest incidence (15.6% of all mouth-withdraw observations) of the use of mouth-withdraw was with the fruit *Doliocarpus dentatus*. On instances where the monkeys did pick this fruit by mouth, they could be observed to spit out the exocarp after chewing, as is shown in the first sequence in Video 2. There were also instances in which they bit and sucked *Doliocarpus dentatus* to obtain the endocarp while leaving the exocarp hanging on the vine. A representative sequence of fruit bite/suck is shown in the last two sequences of Video 2.

Figure 3

Three Fruit Purchase Strategies Used by Ateles geffroyii for Obtaining Fruit



Note. A. Mouth-withdraw: a spider monkey named Kenya displays a mouth-withdraw in which an individual fruit of *Doliocarpus dentatus* is taken by mouth. B. Grasp-withdraw: a spider monkey named UN displays a grasp-withdraw in which a single *Fictus cotinifolia* fruit is taken with the hand. C. Branch-withdraw: the spider monkey UN displays a branch-withdraw in which a branch containing *Fictus cotinifolia* is pulled by hand toward the mouth so that the fruit can be picked by the mouth. D. The frequencies of three types of fruit purchase out of a total of 2,164 retrieval events observed, illustrating that branch-withdraw was about twice as frequent as grasp-withdraw and mouth-withdraw combined.

Grasp-Withdraw

Grasp-withdraw consists of reaching with a hand to pick fruit. Figure 4 (Video 3) illustrates a representative grasp-withdraw movement. The movement consisted of: (1) directing gaze to the fruit item, (2) advancing a hand (Figure 4A), (3) grasping the fruit (Figure 4B), (4) withdrawing the fruit to the mouth and (5) biting the fruit with the incisors (Figure 4C). Figure 4D gives a kinematic representation of a grasp-withdraw associated with obtaining a small fruit item, *Ficus cotinifolia*. The figure illustrates that the monkey directed gaze to the fruit at about the time that a reach was initiated. Then, after vision was disengaged, the monkey grasped the fruit item and then withdrew the fruit to the mouth to grasp it with the incisors.

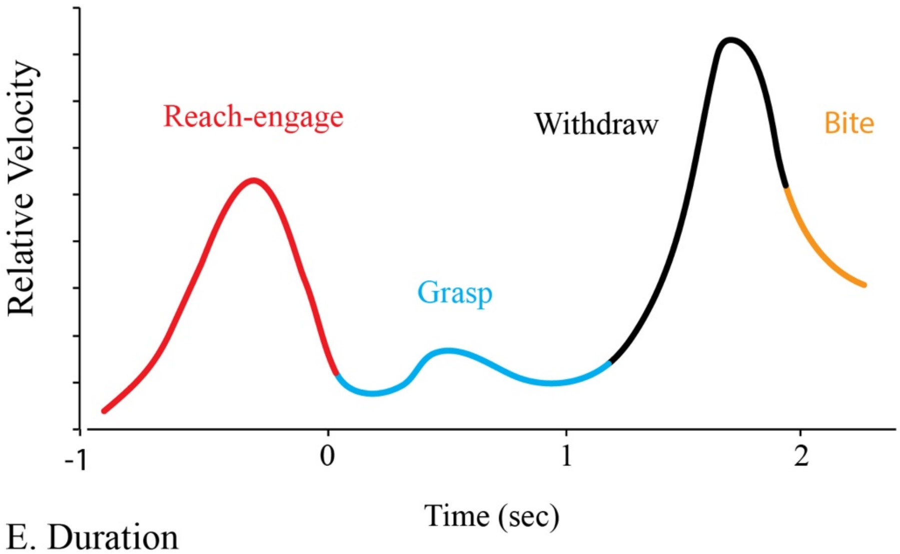
An analysis of the relative duration of each grasp-withdraw component was made from 108 grasp-withdraw movements in which all components could be observed in the video sequence. Figure 4E illustrates the comparison of the duration of the reach, grasp, withdraw and bite movements for the smaller fruit items (>1.5 cm, n = 45) vs the larger fruit items (< 1.5 cm, n = 63). An ANOVA indicated that the time taken to purchase the smaller fruit items was significantly longer than the time taken to purchase the larger fruit items, F(1, 106) = 4.07, $p = .046$, $\eta^2 = .04$, power = 1. There was a significant interaction between duration for the different movement components in relation to fruit size, F(1,106) = 5.93, $p < .001$, $\eta^2 = .04$, power = .74. Follow-up Newman-Keules tests indicated that the time taken to make the grasp of smaller fruit items was longer than the time taken to grasp larger fruit items ($p = .020$). For the other movement components, the reach, withdraw, and bite, the durations were not different in relation to fruit size. Observation of how grasps were made suggested that the longer times taken to grasp a small fruit item was due to the time taken to position the hand in relation to the fruit, using touch cues so that the fingers could close on it (see below).

Figure 4

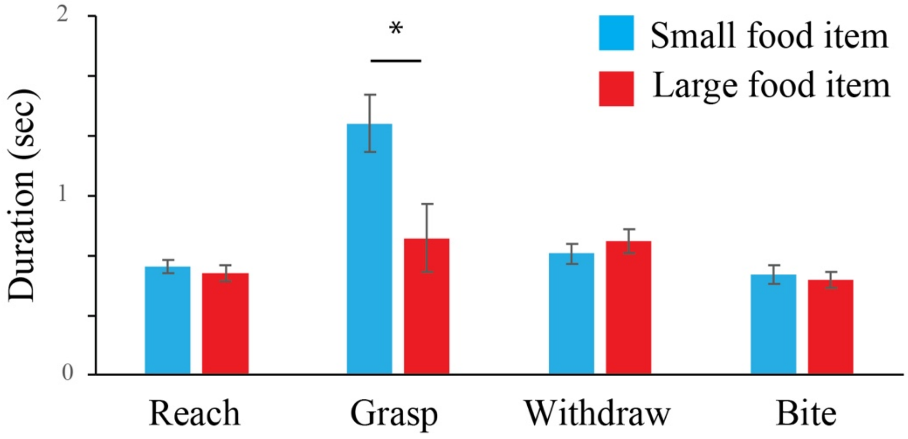
Grasp-Withdraw Reach Made by a Spider Monkey Named Un Eating the Fruit Ficus Cotinifolia

A. Reach B. Grasp C. Withdraw

D. Grasp-withdraw kinematics



E. Duration



Note. The grasp-withdraw movement involves: A. a reach with a hand to take the fruit, B. picking the fruit, C. withdrawing the fruit to the mouth. D. Kinematic representation of a grasp-withdraw for a *Ficus cotinifolia* fruit illustrating the duration of the reach, the grasp, and the withdraw to the mouth. E. Durations (mean±se) of grasp-withdraw movements for small fruit items (< 1.5 cm) vs large fruit items (> 1.5 cm). The grasp duration associated with small fruit items was longer than for the large fruit items, * = $p < .05$.

Branch-Withdraw

Figure 5 (Video 4) illustrates the components of a branch-withdraw movement to obtaining *Ficus cotinifolia,* a small fruit item. Components are grasping a branch containing a target fruit with one hand (Figure 5A), withdrawing the branch toward the mouth (Figure 5B), then reaching with the mouth to take a target fruit item from the branch with the incisors (Figure 5C). A kinematic representation of this sequence is shown in Figure 5D. The knuckle of the second digit of the hand holding the branch and the middle of the upper lip are digitized. The kinematic representation shows that as the branch is withdrawn, the head orients toward the fruit, the fruit is visually engaged, the mouth is advanced to take the fruit, while at the same time disengaging vision, and then using the incisors take the fruit.

It was difficult to observe all gaze features associated with branch-withdraw movements because when the face was inclined, the eyes were obscured against the dark facial fur of the spider monkeys. Nevertheless, 27 branch-withdraw movements were identified in which the eyes were clearly visible throughout the movement sequence. On 23 of these occasions, the monkeys disengaged gaze with a blink before opening the mouth to grasp the fruit with the incisors. Figure 5E illustrates the average duration of branch-withdraw component movements. An ANOVA on component durations of gaze, withdraw with gaze, withdraw without gaze, and bite with the incisors gave a significant effect, F(1,26) = 49.9, $p < .001$, $\eta^2 = .66$, power = .98. Newman-Keules tests indicate that the bite duration (time from the lip touching the food to its removal from the hand) was the component that took the longest to complete, $p < .001$.

Figure 6 illustrates the relative use of branch-withdraw movements in relation to the total number of fruit grasp movements for the 14 different fruits. Figure 6A illustrates the percent of branch-withdraw movements for each fruit. Figure 6B shows there was a significant correlation between fruit size and the incidence of a branch-withdraw, Pearson r = .69, F(1,12) = 11.4, $p = .006$, with branch-withdraw more likely to be used for small fruit items.

On 32 of the 1338 branch-withdraw movements observed, the food was picked with the other hand and not the mouth. For these observations, however, it was difficult to determine the extent to which a monkey was withdrawing a branch as opposed to holding onto it for support.

In sum, these results suggest that grasp-withdraw movements were used in order to assist the mouth in obtaining the smallest fruit items. These were the most difficult to grasp by hand and the most difficulty to transfer from the hand to the mouth.

Inhand-Withdraw Movements

Inhand-withdraw movements, in which a fruit held in the hand is brought to the mouth (Figure 7, Video 5), were only observed during eating of the fruit *Guazuma ulmifolia* (n = 155 representing an average of 21.1 observations in each of 7 spider monkeys. *Guazuma ulmifolia* is a 2-3cm long fruit featuring a hard exocarp that surrounds an endocarp of seeds, which are the targets of eating (Manríquez-Mendoza et al., 2011; Pereira et al, 2019).

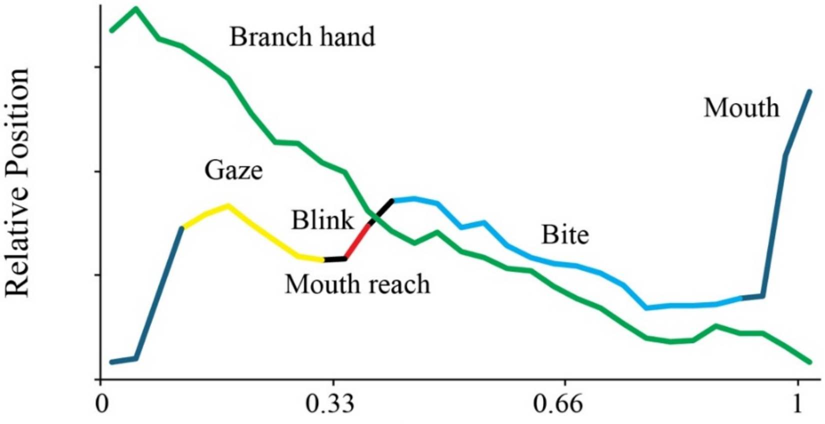
Figure 7 shows a representative inhand-withdraw movement, which consists of first looking at the fruit (Figure 7A), then bringing it to the mouth under gaze (Figure 7B), and then disengaging vision while completing the withdraw movement to the mouth for biting (Figure 7C). A representative kinematic description of an inhand-withdraw is shown in Figure 7D, illustrating its four components: (1) gaze directed at the fruit held in the hand, (2) gaze during the first portion of withdraw, (3) gaze disengage during the second part of the withdraw and (4) grasping with the incisors and chewing with the premolar teeth. Of the 155 inhand-withdraw movements, the eyes were clearly visible in 97 movements, and of these, 96 were associated with a blink at gaze disengage. Associated with the gaze disengage, the head was raised so that when the fruit reached the mouth, the mouth was in a horizontal orientation. After chewing the fruit with the premolars, the spider monkeys spat out the exocarp and then swallowed the endocarp. Figure 7E illustrates the relative duration of each component movement, showing that the movement component with the longest duration was biting and chewing the fruit (F(1,153) = 193.9, $p < .001$, $\eta 2$=.560, power = 1).

Figure 5

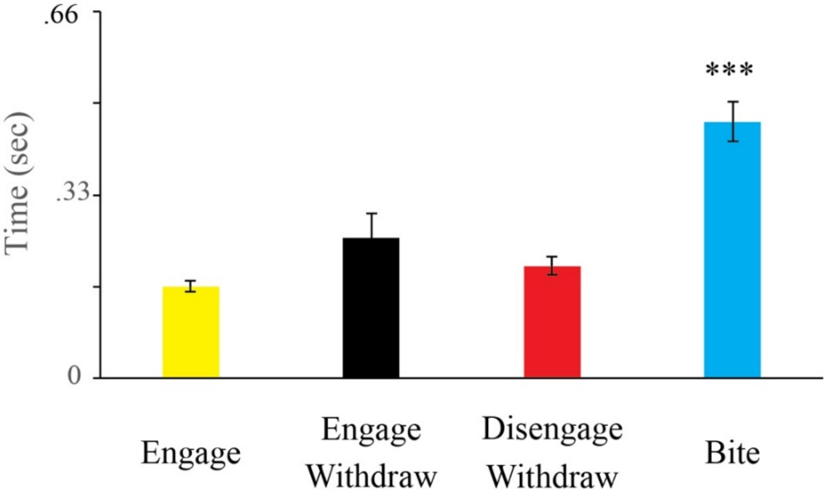
Branch-Withdraw Movement Made by a Spider Monkey Un Eating The Fruit Ficus Cotinifolia

A. Gaze B. Blink C. Bite

D. Mouth Reach



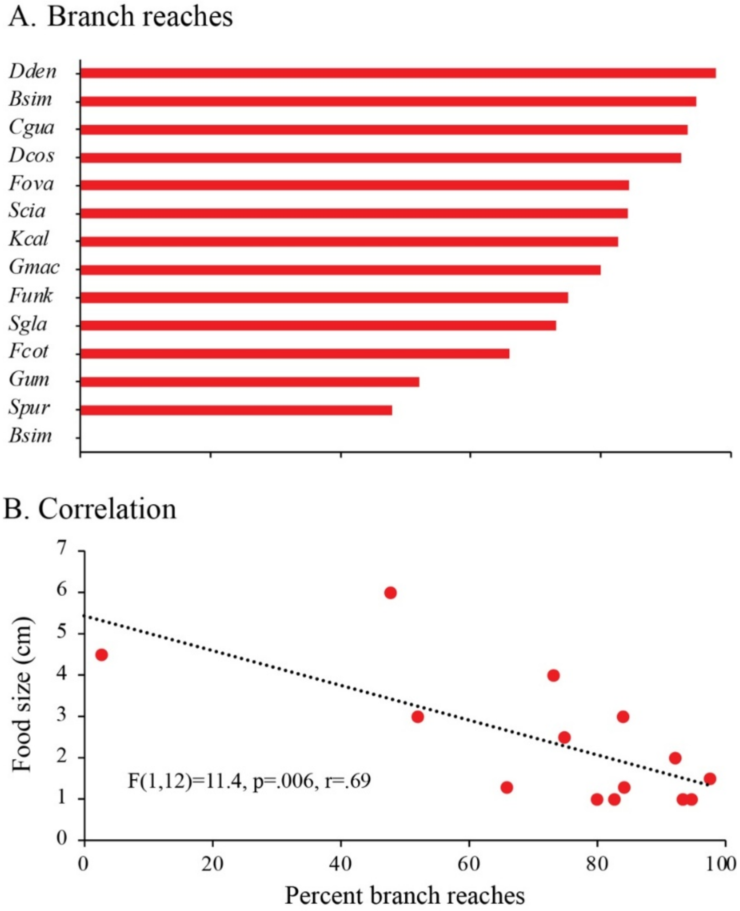
E. Component duration



Note. The branch-withdraw movement involves: A. Directing gaze toward the fruit as the mouth begins its advance to take the fruit; B. Blinking with gaze disengagement as the mouth becomes proximal to the fruit; C. Picking the fruit by advancing the head to bite the fruit with the incisors. D. Kinematic representation of a branch-withdraw for a *Ficus cotinifolia* fruit illustrating the movement of the hand grasping the branch (the knuckle of the second digit is digitized) and the movement of the mouth (middle of the upper lip is digitized) to grasp the fruit. For the bite, the movement of the fruit and the mouth are roughly parallel. E. Duration (mean±se) of the components of branch-withdraw movements of the mouth to take fruit obtained from 28 branch-withdraw reaches. The component that takes the longest to complete is the bite, ***= $p < .001$.

Figure 6

The Percent of All Fruit Retrieval Events that were Branch-Withdraw Reaches as a Function of Fruit Species

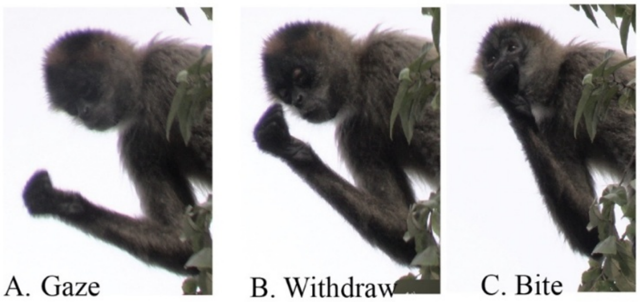


Note. A. The probability of using a branch-withdraw strategy of fruit retrieval as a function of fruit species diameter. B. Correlation between branch-withdraw strategy and fruit species size. The smallest fruit were the most likely to be associated with a branch-withdraw strategy. Food items were: *Doliocarpus dentatus* (*Dcec*), *Bursera simaruba* (*Bsim*), *Coccoloba guanacastensis* (*Cogu*), *Dipterodendrum costaricensis* (*Dcos*), *Fictus ovalis* (*Fova*), *Sciadodendron excelsum* (*Sexc*), *Karwinskia calderonii* (*Kcalcm*), *Guettarda macrosperma* (*Gmac*), *Ficus unknown* (*Fun*), *Simarouba glauca* (*Sgla*), *Ficus cotinifolia* (*Fcot*), *Guazuma ulmifolia* (*Gulm*), *Spondias mombinplumieri* (*Bplum*), *Bromelia plumieri* (*Bplum*).

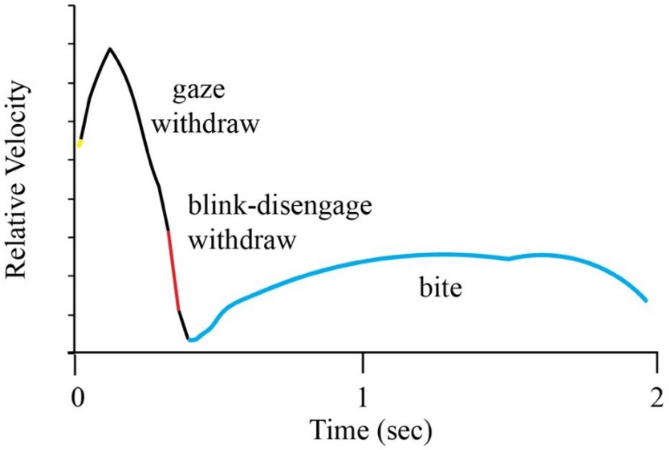
Figure 7

Inhand-Withdraw by a Spider Monkey Named Ajka Eating the Fruit Guazuma Ulmifolia

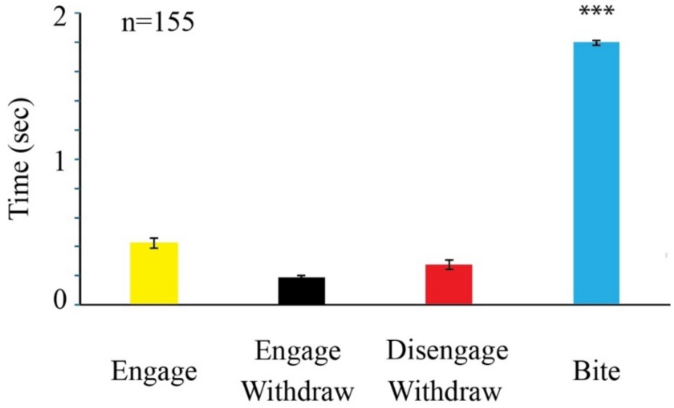
A. Inhand-withdraw



D. Inhand-withdraw kinematics



E. Inhand-withdraw component duration



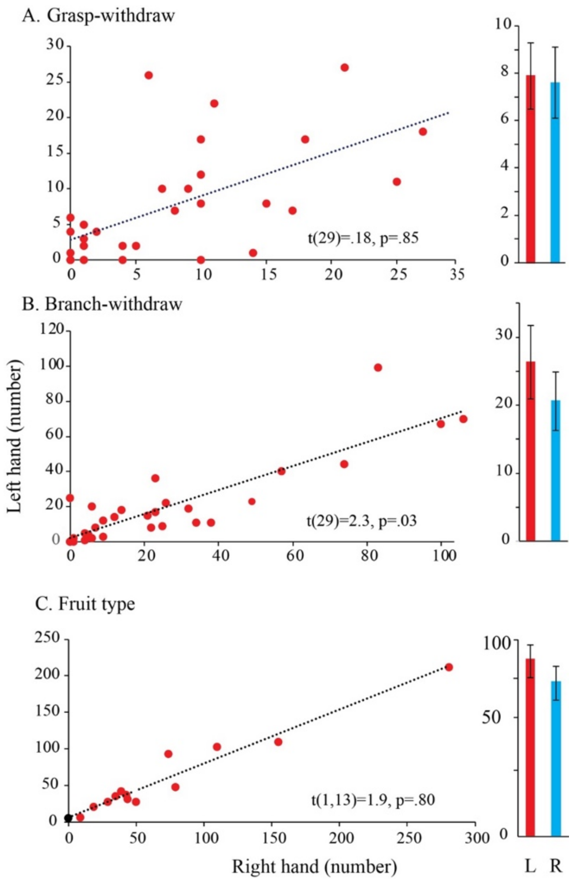
Note. The fruit is held in the hand and brought to the mouth for eating in each inhand-withdraw. The movement consists of: A. Directing gaze toward the fruit held in the hand; B. Withdrawing the fruit toward the mouth while maintaining gaze on the fruit; C. Disengaging gaze from the fruit and concurrently raising the head so that the mouth is in a horizontal orientation to receive the fruit from the hand. D. The relative velocity and duration of the hand's component movements of reach, grasp and bite during an inhand-withdraw that brings the hand to the mouth for chewing. Note: the monkey blinks as gaze is disengaged from the fruit, and the bite duration is relatively long with the hand moving the fruit between the incisor and premolar teeth for chewing. Bottom, E. Relative duration (mean±se) of the component movements of inhand-withdraw movements observed in seven spider monkeys eating the fruit Guazuma ulmifolia. Note: the bite takes longer than the other movements, *** = $p < .001$.

Population and Individual Handedness

Figure 8 summarizes comparisons of left-hand vs right-hand use for picking fruit by 30 spider monkeys. Analysis of the frequence of hand preference for picking and handling fruit gave support for individual left or right-hand preferences but little support for a population hand-preference. Analysis of left and right-hand use, assessed with t-tests for correlated groups, gave no significant difference for grasp-withdraw movements, Student's t(29) = .18, *p* = .850. Individual animals did show preferences in the use of one or the other hand as shown by scatter plots of handedness scores (Figure 8A). Analysis of left vs right hand use for reaching for branches as a part of branch-withdraw movements did produce a small left-hand preference. Student's t(29) = 2.3, *p* = .030, but again there were large individual differences in hand preferences (Figure 8B). Comparisons of hand preference for inhand-withdraw from the seven spider monkeys eating *Guazuma ulmifolia* gave no significant preference in use of either hand, Student's t(6) =12., *p* = .260. When the incidence of left and right hand use was summed for the three types of hand movement, in relation to the 14 different fruit species, there was no left vs right-hand preference, F(1,13) = 1.9, *p* = .08, $n^2 = .22$, power = .15, although there were individual preferences, as illustrated by the scatter plot (Figure 8C).

Figure 8

Relative Use of the Left and Right Hands of Individual Ateles geoffroyi



Note. Scatter plots present left vs right hand use for each individual animal observed eating. Bar graphs give group left vs right hand use (mean±se). A. Grasp-withdraw reaches, in which a fruit item is taken by a hand. B. Branch-withdraw reaches, in which a branch is grasped in one hand and brought toward the mouth with the fruit taken from the branch by the mouth. C. Relative left vs right hand use for all reaches in relation to each of 12 different kinds of fruit species. The spider monkeys displayed very small to no preference for using either the left or right hands when purchasing fruit.

Components Movements of Food Acquisition

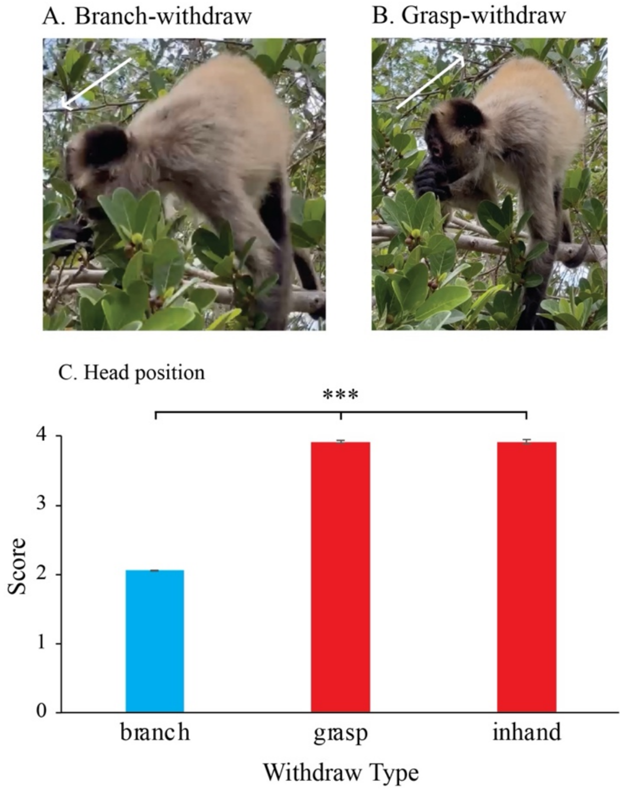
Associated with the use of different food reaching strategies, the spider monkeys made different use of component movements. including use of the mouth for picking, the incisors for grasping, the molars in processing fruit and rotatory movements of the hands and mouth for grasping and transferring fruit from the hands to the mouth. These are described in turn.

Head Movement

Figure 9A illustrates two different head movements related grasping food with the incisors.

Figure 9

A Spider Monkey Called Quetzaltenango Displays Two Kinds of Head Movements Related to Fruit Purchase



Note. A. Branch-withdraw reach for the fruit *Fictus cotinifolia* involves head advance to take the fruit by mouth. B. Grasp-withdraw movement for the fruit item involves head raising to take the fruit, thus withdrawing the mouth away from the hand as it approaches. C. Scores (mean±se) of head movements for all spider monkeys displaying branch-withdraw, grasp-withdraw, and inhand-withdraw movements. Note: The head is advanced to take fruit into the mouth only when making branch-withdraw food purchases, *** = $p < .001$.

The head was advanced to grasp fruit associated with branch-withdraw and it was retracting to accept food associated with grasp-withdraw. Figure 9B summarizes the 5-point score based on 565 branch-withdraw, 234 grasp-withdraw, and 219 inhand-withdraw movements. A repeated measures ANOVA of head movement direction associated with withdraw gave a significant effect, F(2,1012) = 327, $p < .001$, $\eta^{2=}$.86. power = 1. Follow-up Neuman-Keul tests ($p < .001$) confirmed that branch-withdraw movements were always associated with the head moving to take the fruit, whereas grasp-withdraw and inhand-withdraw movements were always associated with the head moving away from the fruit as the hand brought the fruit to the mouth.

Fruit Chewing

An example of fruit chewing is shown in Video 6. Of the 863 observations in which there was a clear view of a monkey placing food in the mouth, 838 featured the spider monkeys chewing the fruit. On 25 of the remaining food placements, the mouth was obscured by head turning or by leaves. Thus, the spider monkeys chewed fruit of all sizes as confirmed by a nonsignificant correlation of chewing with fruit size and type, Pearson r (1,12) = .180, $p = .54$. For larger fruit items, such as *Spondias purpurea*, a small plum-sized fruit, the spider monkeys were also seen to raise the head as chewing progressed, to seemingly aid in swallowing (Video 7). For some other fruit items, notably *Guazuma ulmifolia* and *Ficus cotinifolia*, both of which appeared to have seeds, chewing appeared to be directed to removing the exocarp, which was then ejected by spitting. Occasionally after taking a fruit item into its mouth, the spider monkey simply spat the fruit out, suggesting that in addition to sniffing, taste was also used to assess edibility/ripeness (Melin et al, 2019). When harvesting *Doliocarpus dentatus*, spider monkeys were observed to pick the fruit by mouth and spit out the exocarp after chewing as well as to chew the fruit on the vine, leaving the exocarp still attached to the vine.

Hand Supination and Pronation

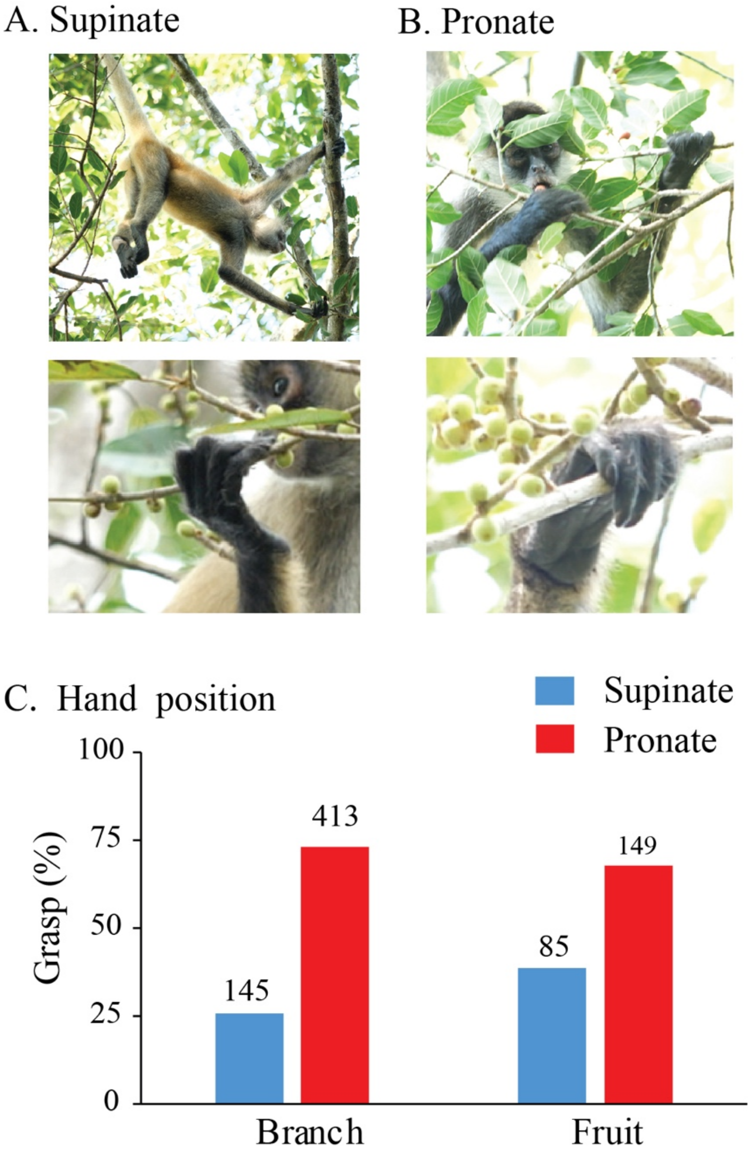
Figure 10 summarizes rotation of the hand associated with 792 branch-withdraw grasps and 562 grasp-withdraw grasps. When grasping a branch, the hand was pronated on 74% of branch-withdraws; that is, palm-up in relation to the target (Figure 10A). When grasping a fruit item, the hand was pronated on 63.6% of grasp-withdraws (Figure 10B). In addition, with respect of the direction of reaches, 66% of downward reaches featured pronation, 63% of horizontal reaches featured pronation, and 78% for upward reaches featured pronation. In all, although pronation was favored as a reach orientation, the choice of hand orientation seemed opportunistic, that is; influenced by the location of the target in relation to the monkey, and not to constraints on hand rotation. Whether pronated or supinated, hand harvesting associated with picking seemed directed to twisting and snapping the fruit free from the branch, as opposed to pulling it free from the branch.

Hand Grasps and Mouth Presentation

Figure 11 (Video 8) illustrates a representative hand posture used by a spider monkey grasping a fruit item followed by a representative hand posture used for presenting that fruit item to the mouth. The details of how a grasp was made were obtained from the observation of 66 grasps of small fruit items (< 1.5 cm) and 45 large fruit items (> 1.5 cm). All grasps were made with the radial side of the hand, with smaller fruit items held between the second digit (index) and the radial thenar part of the palm (Figure 11B). Larger food items were additionally held with the third digit pressing the food item against the palm. A grasped food item was always visible when the hand was viewed from its radial side (Figure 11B), as is also apparent in video of Nelson et al (2024) for a spider monkey grasping a small food item from a tabletop. We have previously designated grasps made between select digits pads and the palm as precision-power grips (Whishaw et al, 2024a,b). When a food item was grasped using a pronated hand, the hand was counter-rotated to fit the food item into the hand. When a food item was grasped using a supinated hand, the hand was positioned so that the food item was in contact with the palm before the fingers were closed for purchase. Food presentations to the mouth were made with the radial side of the hand brought adjacent to the mouth where a fruit item was taken by the incisors (Figure 11C, n = 989/993 observations).

Figure 10

A Spider Monkey Called Kenya Displays Hand Supinate and Pronate Associated with Picking Fruit or Grasping Branches Containing Fruit



Note. A. The spider monkey reaches with a supinated hand to take a *Fictus cotinifolia* fruit item from a branch, as shown in whole body (top) and close-up (bottom) hand views. B. A pronated hand used when grasping a branch in a branch-withdraw to obtain the fruit *Fictus ovalis,* as shown in whole body (top) and close-up (bottom) views. C. The relative use of hand supination and pronation by the spider monkeys associated with branch-withdraw and grasp-withdraw movements showing that both are used but there is a preference for pronation-related grasp movements.

Figure 11

Grasp-Withdraw Hand Posture Used for Fruit Picking and Mouth Placement the Spider Monkey Ucrania

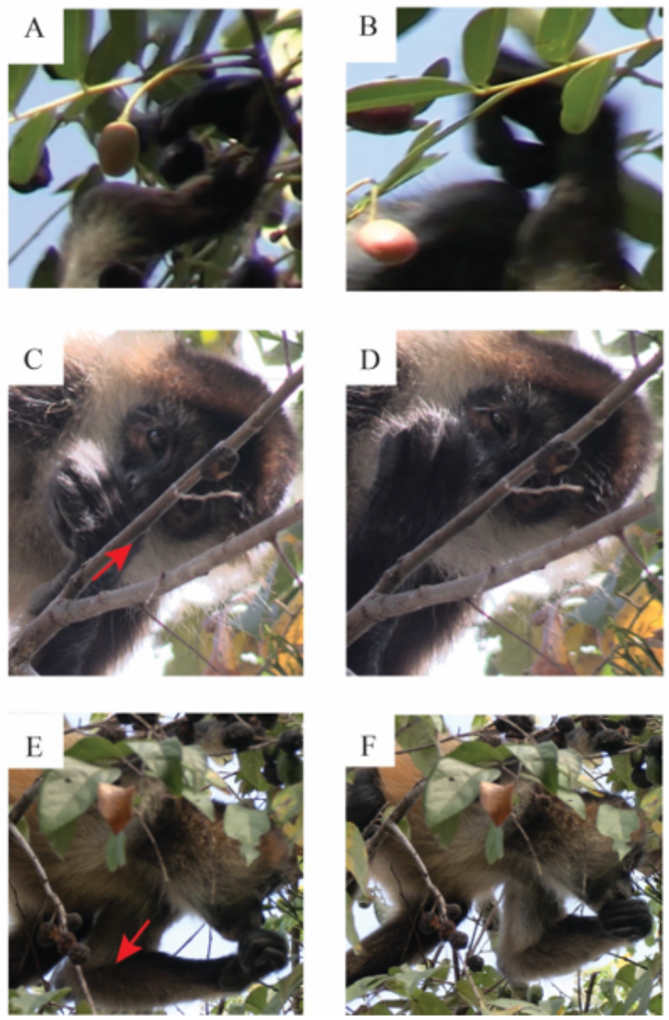
Note. A. Reaching for a fruit item of *Fictus cotinifolia*. B. Grasping fruit using a precision-power grip, in which the second digit pad holds the fruit against the radial side of the palm, with the fruit visible on the radial side of the palm. C. Placing fruit in the mouth with the radial side of the hand juxtaposed to the mouth and the hand in a vertically oriented posture.

Many rotational movements of the hand were associated with each transfer of a food item from the hand to the mouth (Figure 12). Figure 12A shows a large fruit item, *Simarouba glauca*, grasped by a spider monkey with opposition between the palm and digits 2-3. Figure 12B shows the fruit presented to mouth by the radial side of the hand. A radial view of the hand showed that the fruit was visible, and so likely accessible for transfer from the radial side of the hand to the mouth. Nevertheless, to assist in removing the fruit from the hand to the incisor teeth, the spider monkeys made rotational movements at the wrist (Figure 11C,D) and the upper arm (Figure 12 E,F) and the mouth. These rotation movements were not counted but were observed to occur in various configurations in all of 989 observations of food transfer to the incisors.

Presentation of a food item to the side of the mouth so that it could be taken with the premolar teeth was observed on only three in hand-withdraws in one spider monkey eating the fruit *Guauma ulmifolia.*

Figure 12

Grasp-withdraw Hand Posture used for Fruit picking and Mouth Placement by the Spider Monkey Bergen



Note. A. Reaching for a fruit item of *Simarouba glauca*. B. The monkey uses a precision-power grip, in which the second digit holds the fruit against the radial side of the palm, with the fruit visible on the radial side of the palm. C. The monkey places the fruit in the mouth with the radial side of the hand juxtaposed to the mouth with the hand in a vertically oriented posture. C-D. To aid in extracting the food item from the hand, the spider monkey makes supination-pronation hand movements around the wrist, as shown by the arrow, that expose the fruit item to the mouth for grasping. E-F. To aid in extracting the food item from the hand, the spider monkey makes movements around the upper arm, as shown by the arrow, to change the vertical orientation of the hand to expose the fruit item to the mouth for grasping.

Discussion

This study examined the use of visually guided reach and grasp movements in Costa Rican spider monkeys (*Ateles geoffroyi*) foraging in the upper tree canopy. In 79% of observations, spider monkeys used their mouth to pick fruit. Most mouth grasps occurred after the monkeys grasped a branch by hand and guided the fruit it contained toward the mouth. Extension of the mouth to grasp a fruit item was guided by foveal vision, whereas hand use for branch guidance seemingly relied on peripheral vision. When picking fruit directly by hand (21% of observations), the reach was guided by foveal vision. A power grip guided by touch was used to grasp the fruit. Long arms and fingers, augmented by prehensile tail support, extended the distance of reaches into the distal small branches of the canopy. The combination of spider monkey behavior and morphology supports the theory that the reach and the grasp are under separate visuomotor control, with spider monkeys exhibiting a reach phenotype that provides privileged access to fruit on the small distal branches of the canopy.

The dual visuomotor channel theory proposes that in catarrhines, foveal vision guides a forelimb reach to a target's location and then guides the fingers to perform a thumb pad–to–finger pad precision grasp depending upon object configurations (Grant & Conway, 2019; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Karl & Whishaw, 2013; Knecht, 2000; Marzke, 1971; Nashner et al., 1985; Sartori et al., 2015; Whishaw et al., 2019, 2025). Support for the theory has largely come from laboratory studies, but we propose that natural foraging behavior in primates can also serve as a valuable test. Vision, as characterized by retinal pigment variation, plays an important role in platyrrhine fruit picking, including that of spider monkeys (Melin et al., 2004; Riba-Hernández et al., 2024). Here, we found that spider monkeys show a novel division of visual labor during fruit picking: they use foveal vision to guide the mouth toward fruit, while peripheral vision facilitates grasping and manipulating branches. When picking fruit by hand, foveal vision guides the reach, but the grasp relies primarily on touch cues and a power grip. Collectively, spider monkeys exhibit a reach phenotype featuring visual control of the reach—both by hand and mouth—but not of the grasp.

Morphological traits of spider monkeys support the movements featured in the monkey's reach phenotype. Their long arms and fingers, combined with hyperflexible rotational movements at the forelimb joints, allow pronation and supination of the hand to grasp and manipulate branches and to twist fruit free from a branch. Rosenberger et al. (2008) describe forelimb skeletal modifications that enable this hyperflexibility. Spider monkeys are known to use tail support while feeding (Rosenberger et al., 2008; van Roosmalen, 1985; Youlatos et al., 2008), and our quantification shows that up to half of feeding bouts involve hanging by the tail, with no sex or age differences. Even when standing or sitting, the monkeys used tail support while leaning out to reach for fruit. Our conservative definition of tail support required that an animal might fall were tail support removed. Nevertheless, spider monkeys held onto branches with their tails on nearly every reach, suggesting tail prehension aids positional stability in addition to facilitating extended reaches. The combination of long fingers and arms, rotational movements, and tail prehension further all aid a behavioral reach phenotype.

Laboratory studies show that spider monkeys do not perform precision grasps with their hands due to vestigial thumbs (Laska, 1996; Motes Rodrigo et al., 2018; Nelson, 2015a,b, 2024). The SSR population lacks an external thumb (Melin et al., 2022), precluding precision grasping during natural foraging. When making a power grasp, the action was prolonged—especially for small fruits (Figure 4)—due to the time required to orient the hand using tactile cues. Once made, power grasps featured holding fruit between the pads of the second and third fingers and the palm, a grip we term a precision-power grasp (Whishaw et al., 2024a,b). Although the fruit was visible on the radial side of the hand, it was enveloped within the palm. The spider monkeys consistently brought the radial side of the hand to the mouth for food transfer. The transfer was prolonged and required hand and mouth rotational movements to extract the fruit. We suggest that while the absence of a thumb and reliance on a power grip may limit rapid precision grasps and efficient food transfer, these features may aid in positioning branches so that attached fruit is juxtaposed to the mouth. This hypothesis could be tested in other taxa exhibiting convergent thumb reduction, such as colobines and gibbons (Frost, 2015; Van Horn, 1972).

The primary behavioral compensation for the spider monkey's lack of a visually guided grasp is its extensive use of the mouth for fruit picking, which seemingly serves as a shortcut, bypassing the inefficiencies of hand grasps and hand to mouth transfer. Our positional analysis supports this conclusion. Transferring fruit from incisors to molars for chewing did not require the repositioning that occurred when a hand was used. Studies, based on undamaged seeds in scat, have suggested that spider monkeys do not chew (van Roosmalen, 1985); however, we observed consistent chewing of fruit. They also spat out the exocarp of *Guazuma ulmifolia* and *Ficus cotinifolia*, and chewed *Doliocarpus dentatus* on the branch, leaving exocarp attached to the stem. The ability to grasp fruit with incisors and chew with molars in rapid sequence, often while suspended by the tail, was facilitated by a flexible upper body and neck (Rosenberger et al., 2008). Overall, mouth use as the primary grasping organ likely contributes to the efficiency of their reach-centered foraging strategy, enabling rapid fruit consumption while leaving the hands free to reach for branches both for fruit and for support.

Laska's (1996) observation of left-handedness in a laboratory food-reaching task by spider monkeys has not been confirmed by subsequent studies (Hook-Costigan et al., 1996; Motes Rodrigo et al., 2018; Nelson et al., 2015a, 2015b). Nevertheless, the spider monkey's reach phenotype in natural foraging allows revisiting MacNeilage's (1987) prediction that natural foraging should feature a left-hand reach preference. Although spider monkeys are reach specialists, neither their reach for branches nor fruit showed population-level asymmetry, although individual asymmetries were present, consistent with lab findings. They also showed no population-level asymmetry when repeatedly bringing *Guazuma ulmifolia* to the mouth, unlike humans who display lateralization for the same act (Whishaw et al., 2025). Thus, while spider monkeys are reach specialists, they display only individual hand preferences.

A reach-centered phenotype may confer a foraging advantage over other frugivorous primates, such as their sympatric canopy competitor, the capuchin monkey—a species described as the grasp specialist among platyrrhines (Christel & Fragaszy, 2000; Costello & Fragaszy, 1988; Melin et al., 2022; Spinozzi et al., 2004; Truppa et al., 2019, 2021; Whishaw et al., 2024a, 2024b). The spider monkey's extended reach may allow access to fruit that capuchins, adopting sitting or standing postures, cannot reach as easily. The spider monkey's ability to access fine distal branches incapable of supporting their large size further differentiates the species. The contrast between the spider monkey's reach-centered and the capuchin's grasp-centered foraging may exemplify niche partitioning (Finke & Snyder, 2008; Schreier et al., 2009; Ungar, 1996). Although Chapman (1987) questions niche partitioning due to dietary overlap of *Ateles* and *Cebus*, we propose that niche differentiation arises from behavioral distinctions in fruit acquisition rather than diet alone. Future studies could directly compare species-specific reaching strategies and their impact on canopy microhabitat use.

In conclusion, it is relevant to consider whether the spider monkey's reach phenotype is foundational to other behavior, including locomotion. Identifying the order and relative influence of selective agents shaping morphology is challenging but important. Suarez (2006; see also van Roosmalen, 1985) reports that spider monkeys travel among the longest distances of any primate, and Youlatos et al. (2008) describe their locomotion as a forelimb reach strategy assisted by the tail. The present results are consistent with the idea that a tail-assisted suspensory reaching may be an evolutionary precursor to tail-assisted locomotion (Rosenberger et al., 2008; Youlatos et al., 2008). Future anatomical research might explore visuomotor pathway organization in spider monkeys, including corticospinal systems (Bortoff & Strick, 1993; Strick et al., 2021) and their reach-based foraging phenotype. Comparative studies of other atelids (e.g., *Alouatta*, *Brachyteles*, and *Lagothrix*) and taxa with convergent adaptations (e.g., gibbons, colobines) may further illuminate evolutionary exploitations of reach versus grasp phenotypes.

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Supplemental Materials

Video S1

Positional Behavior Facilitated by Tail Grasping

https://doi.org/10.6084/m9.figshare.31288702

Note. A spider monkey called Estados Unidos moves from a head down vertical posture to an almost horizontal position while using both hands to gather fruit-bearing branches to bring fruit to the mouth for mouth-associated fruit picking. Note: Hind limbs are providing minimal support. (30 f/sec).

Video S2

Fruit Picking and Sucking

https://doi.org/10.6084/m9.figshare.31288711

Note. A spider monkey called Kenya takes the fruit *Doliocarpus dentatus* by mouth. The first mouth grasp involves picking the fruit, chewing, and spitting out the shell. The second and third mouth grasps involve taking the fruit in the mouth and chewing/sucking out the pulp while leaving the exocarp attached to the branch. (Slow-motion, 10% of 30 f/sec speed).

Video S3

A Spider Monkey Named Un Makes a Grasp-Withdraw of a Ficus Cotinifolia Fruit Item

https://doi.org/10.6084/m9.figshare.31288717

Note. A. Visual disengage occurs well before the contact of the hand with the fruit item. B. Hand adjustments associated with tactile mediated grasp of the fruit item. C. Presentation of the fruit to the mouth with the radial side of the hand. (Slow-motion, 10% of 30 f/sec speed).

Video S4

A Spider Monkey Named Un Makes a Branch-Withdraw of a Ficus Cotinifolia Fruit Item

https://doi.org/10.6084/m9.figshare.31288720

Note. A. Blink-associated disengage during the reach for the food item. B. The lips and incisors both participate in picking the fruit. C. Mouth adjustments associated with tactile-mediated grasp of the fruit item. (Slow-motion, 10% of 30 f/sec speed).

Video S5

A Spider Monkey Called Ajka Displays an Inhand-Withdraw in which the Fruit Guazuma Ulmifolia is Held in Hand and then Brought to the Mouth for Chewing to Remove the Shell

https://doi.org/10.6084/m9.figshare.31288723

Note. A. The inhand-withdraw movement consisted of a number of movement components: A. Directing gaze to the fruit item and withdrawing the hand toward the mouth; B. Disengaging gaze with a blink when completing the withdrawal of the hand toward the mouth; and C. Grasping the fruit with the mouth from the radial side of the hand and releasing the fruit to be taken with the incisors. (Slow-motion, 10% of 30 f/sec speed).

Video S6

Fruit Chewing

https://doi.org/10.6084/m9.figshare.31288726

Note. A spider monkey called Kenya displays fruit chewing during successive grasp-withdraw and branch-withdraw movements for the fruit *Ficus ovalis*. (Slow-motion, 10% of 30 f/sec speed).

Video S7

Mouth-Withdraw

https://doi.org/10.6084/m9.figshare.31288729

Note. A spider-monkey called Poltava reaches for the fruit *Simarouba glauca* by mouth. After chewing the fruit, the spider-monkey raises its head to swallow the fruit (Slow-motion, 10% of 30 f/sec speed).

Video S8

Grasp-Withdraw Grasp

https://doi.org/10.6084/m9.figshare.31288732

Note. A spider monkey called UN makes a grasp of the fruit item *Ficus cotinifolia*. Note A. Touch is used to place the radial side of the palm (thenar pads) on the fruit. B. The hand is counter-rotated to bring the second digit into position to grasp the fig against the palm. C. The fig is visible on the radial side of the hand. (Slow-motion, 10% of 30 f/sec speed).