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The Exclusive Use of a Reach versus a Grasp When Foraging by the Mantled Howler Monkey (*Alouatta palliata*)

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Abstract – Howler monkeys (*Alouatta*) are characterized as energy minimizers, featuring a reduced daily foraging range, an above-branch quadrupedal positional repertoire and a reduced forelimb motion. The present study quantifies how these behavioral features influence the reach and grasp of the mantled howler monkey (*Alouatta palliata*) for harvesting a diet of leaves, fruit, flowers and vines. Wild howler monkeys, habituated to human observers, were filmed in Sector Santa Rosa (SSR), Área de Conservación Guanacaste in northwestern Costa Rica. Video recordings of the monkeys harvesting 20 food species were subject to frame-by-frame analysis. The monkeys suspended themselves by their tail for 58% of 2208 reaches. On 99% of reaches they hooked a branch with a power grasp and pulled it toward their mouth. Reaching for a branch featured a pronated hand and upper arm abduction/adduction with minimal hand or arm rotation. Fruit and flowers were plucked from the branch using the incisors and leaves were plucked using the molars. Plucking a food item from a branch was aided by lower arm extension that relaxed the hand's pull on a branch, allowing the recoil of the branch to jerk the food from the branch. Independent grasps by hand (249 observations) were only used to adjust food in the mouth or take food from the mouth to reorient it for selective biting. Howler monkey tail prehension and branch withdraw feeding thus represents an almost exclusive use of a reach strategy with little/no use of an independent grasp by the hands or mouth. In requiring little hand or finger skill, branch pulling may contribute to the howler monkey's energy minimizing lifestyle. This reduced motoric commitment to eating may enable a concordant reduction in brain size as a further source of energy minimization. The findings support the idea that variation in the use of the reach and the grasp contribute to the feeding diversity of primates.

Keywords – Branch pulling, Dual visuomotor theory, reaching, hand use, prehension, teeth grasps, positional behavior, folivory, energy minimizing

Hands skills are central to the feeding of many terrestrial vertebrates (Iwaniuk and Whishaw, 2000a; Sustaita et al., 2013). Primates are especially skilled in their hand movements, with humans evolving the most elaborate and skilled movements of the hands and fingers (Napier & Tuttle, 2021; Covarrubias et al., 2026). As noted by Kinsey (1986), the study of the platyrrhine primates has been relatively neglected in the search for evidence that can inform an understanding of the evolution of human hand movements. This primate parvorder shares a relatively distant last common ancestor (LCA) with humans, which is further removed than the LCA humans share with catarrhine monkeys. Nevertheless, parallelisms in hand use by platyrrhine primates can potentially clarify general principles of hand movement relevant to all primates.

One principle of interest is the neural organization proposed by Jeannerod's dual visuomotor channel theory of reaching (Jeannerod, 1981; Jeannerod et al., 1995, 1998). The theory proposes that one neural channel, or pathway, from visual to motor regions of the brain, controls the reach to bring a hand to a spatial location of a target. The second neural channel controls the grasp, which involves hand rotation and finger shaping proportional to the size and shape of a target. In humans, evidence supporting the theory comes from measures of the hand and finger movement in experimental studies, in the analyses of neural activity and in the study of brain injuries that selectively affect one or the other visuomotor channel (Grant & Conway, 2019; Goodale et al., 1994; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Karl & Whishaw, 2013; Hoff & Arbib, 2000, 1971; Sartori et al., 2015; Whishaw et al., 2019, 2025). Comparative studies of visual control of reaching in nonhuman primates provides evidence from which the evolutionary history of these visuomotor channels can be inferred (Napier, 1956; 1962; Karl and Whishaw, 2013; Whishaw and Karl, 2019). The strepsirrhines, an early-branching primate suborder, display a reach strategy with little finger shaping when grasping (Peckre et al., 2019, 2023). Catarrhine primates, such as macaques (genus *Macaca*), in addition to reaching, display finger shaping in making precision grips with which they take objects between the thumb and finger pads (Hirsche et al., 2022; Macfarlane & Graziano, 2009; Marzke, 1971; Pouydebat et al., 2008; Scott, 2019). Hand use by platyrrhines suggest that their reaching may be similarly controlled by these two visuomotor channels. *Cebus imitator* use finger shaping to grasp and handle objects, pick fruit from tree branches, and use tools, although they do not make true precision grips involving thumb–finger pad opposition (Barrett et al., 2018; Christel, 1993; Christel & Fragaszy, 2000; Whishaw et al., 2024a, 2024b; Truppa et al., 2019; 2021). In contrast, spider monkeys, *Ateles geoffroyi*, which are sympatric with *Cebus imitator* throughout their range (Alfaro et al., 2015), are more specialized in using a reach strategy. Their long arms and fingers and suspension by their prehensile tail contribute to extending reaches for fruit into the small distal branches of trees (Whishaw et al, 2026). These family differences suggest that the study of other platyrrhines could further clarify the adaptions of the reach and grasp in platyrrhine foraging.

Howler monkeys, genus *Alouatta*, were the first of the 4 genera of the atelid monkeys to differentiate (Hartwig et al., 2011; Rosenberger & Strier, 1989). Consequently, their reaching abilities could be conserved, and so be similar to spider monkeys, thus representing the stem characteristics of the family *Atelidae*. Alternately their reaching ability could feature derived characteristics (Jones, 2008); that is, novel characteristics that evolved after they separated from their ancestral group. Howler monkeys are large-bodied platyrrhine primates, characterized by an energy minimizing behavioral lifestyle featuring a small day and home range (Cortés-Ortiz et al, 2003; Di Fiore and Saurez, 2007; Fortes et al., 2014; Youlatos et al., 2015). The Mesoamerican mantled howler monkey, *Alouatta palliata,* is among the most folivorous of platyrrhines (Chaves et al., 2013; Dias & Rangel-Negrín, 2014; Gisbrecht et al., 2025). Because howler monkeys also eat fruit, Rosenberger et al (2011) characterize their foraging as semifolivory. They eat nearly all available plant parts in their habitats, using at least 1,165 plant species belonging to 479 genera and 111 families (Belmont et al., 2025; Dias et al., 2014; Glander 1975; Melin et al., 2017; Milton, 1978, 1980). Nevertheless, they adapt to food availability. Comparative studies show that only a quarter of food species are common across groups occupying different habitats (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007). Although howler monkeys were among the first platyrrhines to be the subject of behavioral studies (Kinzey, 1986), the study of how they use their hands to eat has been largely anecdotal (Carpenter, 1934; Smith, 1977; Ungar, 1990). Additionally, Youlatos & Guillot (2008) in highlighting their distinct above-branch quadrupedal positional behavior features may have underestimated their forearm mobility. Milton (1978) notes, for example, that they use their prehensile tail to suspend their body while feeding and use their hands to grasp branches and so obtain leaves and fruit.

Here, we perform the first detailed examination of forearm use during foraging behaviour in howler monkeys. Given their distinctive morphology, we expected that the documentation of their positional behavior and their hand control would offer insights into their feeding behavior. We also expected this analysis to give insights into the howler monkey nervous system, which features a brain about half the size of their family member, the similar sized spider monkey (Milton, 1993). We use an experimental design similar to Whishaw et al., (2024a; 2026) in which videos of *Cebus imitator* and *Ateles geoffroyi* engaging

in spontaneous foraging in their natural habitat, were subject to frame-by-frame analysis. We scored their positional behavior and the reach and hand movements that they used to handle/withdraw food items to the mouth for eating. Accordingly, wild and unprovisioned mantled howler monkeys (*Alouatta palliata*), were videorecorded as they foraged for 20 different species of leaves, fruit and flowers. The videos were trimmed to include examples of fruit and leaf picking and eating and were then examined.

Methods

Ethics Statement

Data were collected under Costa Rican research permits R-SINAC-ACG-PI-11-2024; R-SINAC-ACG-PI-24-2025; and ACG-044-2025; and University of Calgary Animal Care Committee ethics permit AC24-0021.

Study Population

The feeding behavior of the Costa Rican mantled howler monkey (*Alouatta palliata palliata)* was filmed in 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 sympatric monkey species is ongoing (Melin et al., 2020). The field site was the same as that in which the reaching and grasping behaviors of sympatric *Cebus imitator* and *Ateles geoffroyi* were recently studied (Whishaw et al., 2024a; 2026). Filming was done from March through August, 2025, which bridges the late dry season (March and April) to the early to mid wet season (May through August). These months are typically associated with moderately high fruit availability. 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 continuous video samples, such that recording was done by videographer standing on the ground, typically between 10-20m from the study subject. Recording was done when there was a relatively unobstructed view of the focal monkey (Melin et al., 2022). The age and sex distribution of 23 monkeys when filmed was: 7 adult male, 9 adult female, 7 juvenile. Individuals were identified to the level of age and sex and were sampled opportunistically, based on visibility. Although the monkeys were not all individually identified, filming in terms of sex and age classes was representative of the population. Each film clip was labeled with the date and tree species on which a monkey was feeding.

Food Items

In addition to documenting behavior, the plant species that the howler monkeys were eating was recorded. There were 19 tree species and 1 vine species. Flowers were consumed from: *Maclura tinctoria*, *Lysiloma divaricatum*, *Bursera simaruba*, *Sideroxylan capiri*. Fruit were consumed from: *Cecropia peltata*, *Sapium glandulosum*, *Simarouba glauca*, *Ficus cotinifolia*, *Sciadodendron excelsum*. Leaves were consumed from: *Tabebuia ochracea*, *Licania arborea*, *Astronium graveolens*, *Trichilia martiana*, *Spondias mombin*, *Chomelia spinosa*, *Ficus hondurensis*, *Brosimum alicastrum*, *Ficus goldmanii*, *Andira inermis*. Vine leaves were: *Forsteronia spicata*.

Video Recording and Analysis

Video recording at 30 frames per sec (fps) using a VIXIA HF G70 camcorder provided *ad libitum* recordings of natural eating behavior. For each video recording session, the field of view was set so that the entire monkey was in view, including its tail and reaching hand. The purpose of having a wide view was to ensure that any support for positional behavior provided by the tail could be documented along with the reach and the consumption of a food item.

We analyzed 214 video clips, which together comprised 3:45 hr of video. The total time of video recording as a function of sex was female = 150 min (17 min for each female), male = 84 min (14 min for each male). Recording time as a function of age was adult = 168 min (13 min for each adult), juvenile 420 min (60 min for each juvenile). Recording time for eating of different food types was: leaves =96 min, fruit = 90 min, flower = 22 min and vines = 4 min). Video recordings were examined frame-by-frame using Quicktime 7.7 and Adobe Premier Pro software on an Apple computer resulting in the examination of 372,600 video frames. Videos were scored using previously described methods (Hirsche et al., 2022; Peckre et al., 2023; Whishaw et al., 2024b). Repeated scoring of the videos was used to describe feeding sequences in which a howler monkey obtained a food item and brought it to its mouth. Because animals were reaching through leaves and adjusting their limbs and tail placement, some movements of reaching were visible at times and others were obscured. The observable components were always scored.

Behavioral Analysis

Positional Behavior

Positional behavior, which includes all postures used by an animal to interact with its environment (Youlatos & Guillot, 2014), was measure as an animal grasped a branch, and then again when they took food into their mouth. These measures were complicated by the many possible configurations of the limbs and tail. Therefore, 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., 2024a). In this system, an animal's body position is described by its orientation in 45^{o} steps around a circle. For example, frequently occurring postures are: the back is horizontal as occurs with a standing posture = "0", leaning down at a slant = "1", hanging straight down = "2", standing straight upright = "6", and sitting with a 450 upward slant = "7". Reach behavior was scored along with positional behavior as follows:

Grasping. An animal received a positional score at the point that it grasped a branch containing a food item.

Consumption. An animal received a positional score at the point that the food item was taken by the mouth.

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.

Food-Purchase Movement

Four types of reaching and laterality were documented by counts of events:

Grasp-withdraw. A grasp-withdraw involved a single hand advancing to grasp a food item from a branch, with the item then brought to the mouth.

Mouth-withdraw. A mouth-withdraw involved the mouth taking a food item 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.

Branch-withdraw. A branch-withdraw involved grasping a branch by hand, which was then brought toward the mouth, so that a food item could be taken from the branch with the mouth or hand.

Hand laterality. Use of the left or the right hand for hand-related reach/withdraw types was counted to determine individual and population hand asymmetry, as has been done in previous studies (Hook-Costigan & Rogers, 1996; Motes Rodrigo et al., 2018; Nelson et al., 2015; Whishaw et al., 2026).

Arm and Head Reaching

The relative contributions of arm vs head movement to reach for a food item was scored on a 5-point scale (Hirsche et al., 2022; Peckre et al., 2023; Whishaw et al., 2026):

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 as it was grasped by the 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 both.

Score 3. Most of the withdraw was accomplished by the hand holding the food item, with only orienting movement made by the mouth toward the hand.

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

Hand Grasps in Relation to Food Items

The relative location of the hand on a branch with respect to the food item, as a monkey made a branch-withdraw movement, was rated on a 3-point scale. This measure also describes the relationship between the grasping hand and the target as it is taken by the mouth.

Score 0. The hand was adjacent to the target item.

Score 1. The hand was at least two hand widths away from the target item.

Score 2. The hand was at a distance approximating the length of the forelimb from the target item.

Hand Rotation

The hand rotation at the point that a branch or food item was grasped was scored using an Eshkol-Wachman (Golani, 1994; Whishaw et al., 2024) numeric-derived system. Thus: "0" represents a pronated (palm-down) position, 1 through 3 represents 45^0 steps of clockwise rotation, and "4" represents a supinated (palm-up) position.

Incisor and Molar Grasping

The relative use of the incisor vs the molar teeth in taking a food item from a branch was scored for each fruit, flower, leaf and vine mouth grasp as follows:

Incisor grasp. An incisor grasp was scored if a food item was brought to the front of the mouth and grasped by the incisor teeth only.

Molar grasp. A molar tooth grasp was scored if a food item was taken by the side of the mouth or if the mouth was fully opened allowing the item to be pushed into the mouth so that the molar teeth could contribute to the grasp.

Hand Grasps

Hand grasps used in foraging were classified using previous descriptions and were documented by counts of occurrences. Reaching movements during which the hand was shaped to grasp and then grasped a food item was scored for the following grasp types. In addition, the point of first contact by the hand with a branch was recorded, when visible. The digits were labelled from D1 (thumb) to D5 (pinkie).

Precision grasp. A precision grasp involved holding an item between the D1 pad and one or more of the distal D2-5 pads (Napier,1956; 1962).

Pseudo-precision grip. A pseudo-precision grip involved holding an item between the sides of D1 and the and D2 (Spinozzi et al., 2004).

Power grasp. A power grasp involved clamping an item between combinations of D1-D5 and the palm, but usually not involving D1 (Napier,1956; 1962).

Precision-power grasp. A precision-power grasp involved holding a food item between one or move digit pads and the palm (Whishaw et al, 2024b; 2026; Wiltshire et al., 2026).

Scissor grip. A scissor grip (also termed zygodactylous or schizodactylous grip) held an item between any of the digits of the hand, but usually between D1-2 on one side of the target and D3-5 on the other side, a grip that howler monkeys use to grasp a branch when walking (Youlatos, 1999).

Movement Kinematics

Kinematic measures of arm, hand and head movement were diagrammed using the open access software program Tracker (https://physlets.org/tracker/). Event time and body, hand and eye coordinates were manually marked frame-by-frame for the duration of a reaching act. Coordinates (x,y) were transferred from Tracker to Microsoft Excel to generate graphical representations as movement velocity. Figures were made in Adobe Illustrator.

Statistical Analyses

Each food retrieval act was counted in terms of the acting animal: e.g., food type, positional behavior, and retrieval type. Posture and hand grasping type are reported as total number of observations per food retrieval act. Conjunctions of behaviors were assessed using the Pearson product-moment correlation. 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. Group numeric comparisons were made with chi-square ($\chi 2$) tests. Laterality measures were made using Student's t-tests with the comparison variable being chance occurrence. The temporal relationship between movements were described kinematically. Statistical values of $p < 0.05$ were considered significant (Cote et al., 2021).

Results

General Foraging Observations

Video footage demonstrated that the howler monkeys harvested leaves, fruits, flowers and vines from tree branches. The howler monkeys displayed an array of body postures for eating and distinctive food purchase strategies. 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 the 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., 2017; 2022). When reaching for the fruit of *Simarouba glauca*, it was observed that the monkeys chose fruit with a deep purple color. When reaching for the leaves of *Ficus goldmanii*, it was noted that the monkeys selected leaves with the lightest green shaded toward yellow, which are younger leaves. These observations support conclusions of visual selectivity in food choice (Melin et al., 2017; 2022; Milton et al., 1980), but because they did not directly influence the selection of reaching movements, they are not documented further here.

The results provided 2,208 examples of reaching behavior to obtain food, with each video clip providing an average of 10.3 individual reaching movements. The number of reaches in relation to the type of food was; leaf = 1078, fruit = 691, flower = 404, vine = 35. The distribution of the number of reaches as

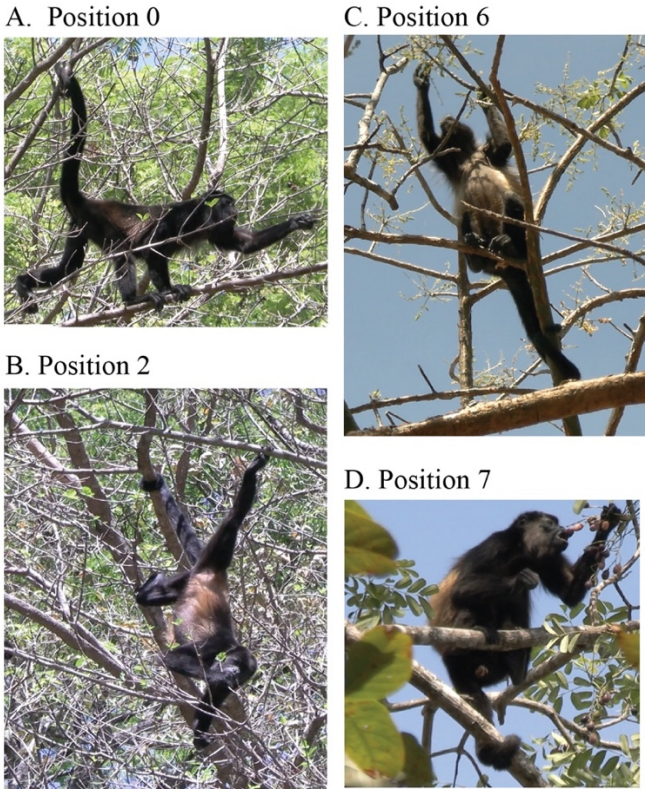
a function sex was; female =1,302, male = 906. The distribution of number of reaches as a function of age gave; adult = 1844, juvenile = 363. Additionally, we made 289 observations that included a hand brought to the mouth to adjust food (140/289), and a hand taking food from the mouth to then bring it back to the mouth for further eating (149/289; i.e., inhand-withdraw movement).

Positional Behavior

Figure 1 illustrates examples and numerical scores for the four positional behaviors that occurred most frequently. These include a horizontal position standing on all fours (position 0), hanging straight down suspended by tail, often with assistance from the other limbs (position 2), standing or sitting straight up (position 6) and sitting in a diagonal position (position 7).

Figure 1

Positional Behavior Displayed by Alouatta palliata as they Pull in a Branch to take Leaves or Fruit from the Branch by Mouth



Note. A. In position 0, the long axis of the body is in a horizontal orientation. B. In position 2 the long axis of the body points straight down. C. In position 6, the long axis of the body points straight up. D. In position 7, the long axis of the body is inclined as the howler monkey adopts a sitting posture. In A and B, the tail is used to assist postural support, in C and D the tail grasps a branch, but postural support is not dependent upon tail grasping.

Figure 2A illustrates the positional scoring system in which positions were notated in relation to the orientation of the long axis of the body, with deviations from a horizontal orientation (score = 0) by successive steps of 45^{o} (thus giving scores 0 through 7).

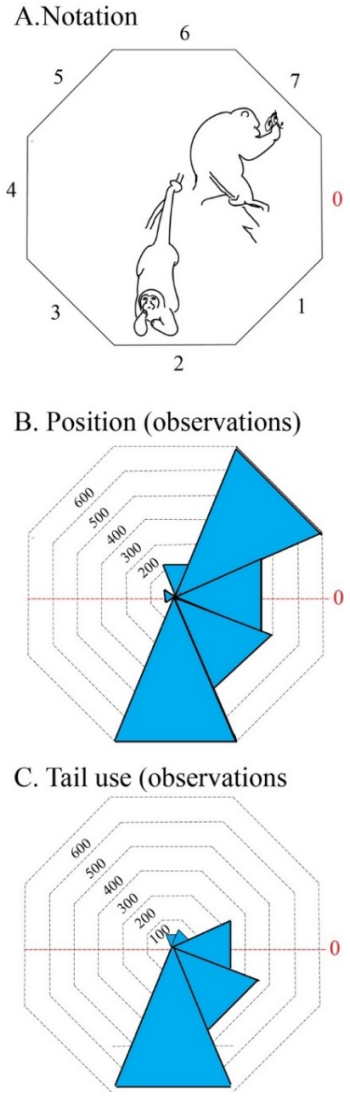
As is shown in Figure 2B, the two most frequent positions were a sitting posture with the body at about a 45^{0} - up angle (position = 7) and hanging by the tail with the head and torso oriented straight down (position = 2). There were also many occasions in which the monkeys adopted a horizontal posture (position

=0) or oblique downward posture (position = 1) or stood straight up (position = 6), and even a few occasions in which they hung by four limbs in an upside-down position (position 4).

Positions were scored when a monkey reached for a branch to bring it toward the mouth and again when they used their mouth to take a food item from the branch (see also Carpenter, 1934). The correlation between positional behavior at the time that a monkey first grasped a branch to bring a food item to the mouth and the point that the monkey bit the food item that it had brought to its mouth was r >.99. Thus, the monkeys did not change positions between reaching for a branch to a food item to the mouth and then reaching and taking the food with the mouth.

Figure 2

Notation Scores of Positional Behavior and Tail use by Alouatta palliata



Note. A. Eschol-Wachmann notation scores of positional behavior in which one of 8 numbers are assigned to the position of the long-axis of the body in relation to position 0, in which the long axis of the body is horizontal. B. Observations of positions when reaching for food. Position 7, a sitting posture, and position 2, a hanging straight down posture, occur most frequently. C. Observations of positional behavior that depend upon the tail support. Compared to the overall incidence of positional use in B, reaching forward in a horizontal orientation, position 0, uses tail support on about one half of observations whereas reaching down obliquely, position 1, and when inverted, position 2, always depended upon tail support. See Figure 1 for photos of representative positions.

As is shown in Figure 2C, some positions were dependent upon tail prehension, in which a monkey held onto a branch with its tail to prevent itself from falling. Of 2208 reaches, prehension for support was used in 57.5% of reaches. Positions requiring tail support included about half of reaches made with the body in a horizontal position (position = 0), in which a monkey leaned out to reach, and all positions in which they reached when inverted (positions 1-2). The monkeys also usually held onto branches with their tail when they adopted postures that did not require support to prevent falling, but these were not documented as postures dependent upon tail support.

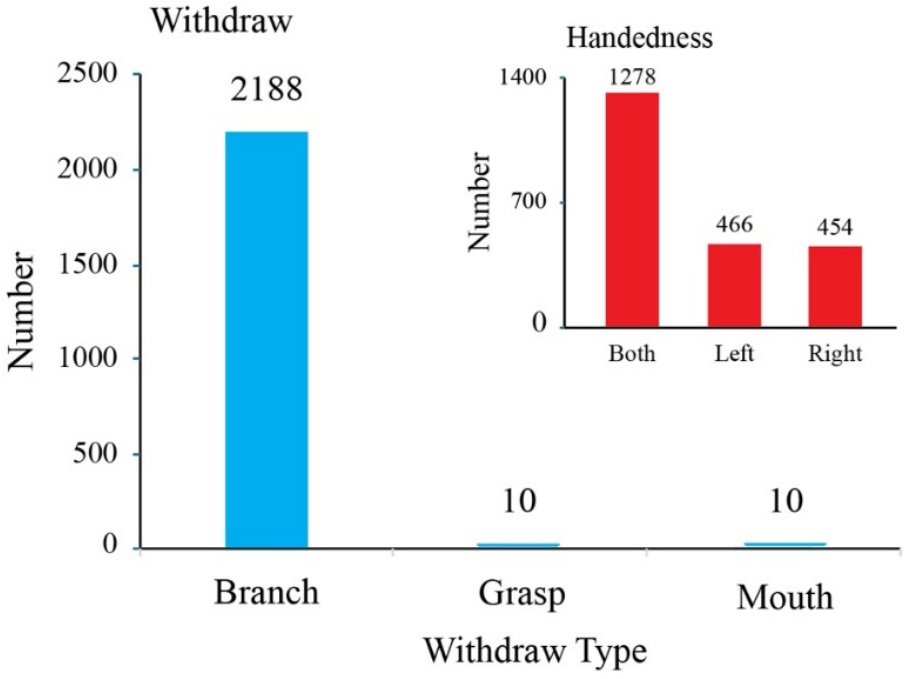
Positional behavior as a function of sex was found to be similar in female vs male monkeys. Percent occurrences of all reaches in different positions for female vs male at the 5 the main positions were: 0 = (19 vs 14,) 1 = (18 vs 16), 2 = (21 vs 37), 6 = (12 vs 9), 7 = (28 vs 25), which resulted in a nonsignificant $\chi^2(4) = 8.42$, p= .20. Positional behavior was also examined as a function of age, which showed that percent occurrences of positions for adult vs juvenile at the 5 most used positions were similar: 0 = (18 vs 16,) 1 = (16 vs 24), 2 = (27 vs 33), 6 = (12 vs 5), 7 = (28 vs 22), which resulted in a nonsignificant $\chi^2(4) = 5.92$, p = .20. Together, these results suggest that body size determined by sex and age were not factors related to the variety of positions from which the monkeys reached for branches, as might occur for other behavior (Goldsborough et al., 2024).

Reaching Movements

The howler monkey's reaching movements were dominated by branch-withdraw movements (Figure 3). There were only few unambiguous occurrences of grasp-withdraw movements, in which only a hand was used to obtain food, or mouth-only grasps, in which food was only picked with the mouth (these exceptions are described below).

Figure 3

Incidence of Withdraw Movements and Handedness



Note. Most reaching movements were branch-withdraw movements, in which a monkey pulled a branch toward the mouth and took food from the branch with the mouth. Withdraw movements in which a monkey used a direct grasp on the food or grasped food only with the mouth were infrequent. Insert. The insert shows branch withdraw movements most frequently featured both hands, with smaller and equal numbers of left and right hand withdraw movements.

Branch-Withdraw Reaches

Figure 3 (Video S1) illustrates that 2178/2208, or 98.6% of reaches observed involved reaching with one or both hands to grasp a branch and pull it toward the mouth. The item that was the target of eating was usually located relatively close to one or the other hand. If more than one food item was taken from one branch, a monkey might alternate mouth reaches in the direction of one or the other hands. It might also manipulate a branch with one hand so that one food item was brought close to the mouth for biting and then manipulate the branch with the other hand so that a different food item was brought close to the mouth for biting. These variations of handling movements were not included in the present analysis.

The insert in Figure 3 shows that most branch-withdraw reaches (66%, insert) involved using both hands to pull a branch. The insert in Figure 3 also gives the count of hand preference when only one hand was used. The left and the right hand were used on a similar number of occasions (466 vs 454). A previous laboratory study of laterality reports a right-hand preference in *Alouatta seniculus* when picking up food from a surface or reaching into a pail, but that study also found that the animals would not reliably perform two other grasping tasks (Sfar et al., 2014). Other studies of laterality in *Alouatta palliata* concerned hand use in grooming (Ortíz-Zárate et al., 2024) or tail positional behavior (Crespo Mingueza, 2015), and these report no group difference, as found here.

The numbers of branch withdraw movements as a percentage of the total number of observations were proportional to the number female vs male monkeys and adult vs juvenile monkeys. Male monkeys made 63.4% and female monkeys made 57% of branch-withdraw movements with two hands and adult monkeys made 62% and juvenile monkeys made 45% of branch-withdraw movements with two hands. The greater frequency of two hand reaches by adult monkeys may have been related to withdrawing larger branches, but this possibility was not investigated. With respect to sex and age measures of handedness for one-hand branch pulls, 52.3% of branch-withdraw acts were made with the left hand by females and 52.5% made by the left hand by males. The adult vs juvenile comparisons of 54.2% vs 48.6 % giving results that were nonsignificant for sex and age, χ^2 (1) = 0.16, p = .69.

Inhand-Withdraw Movements

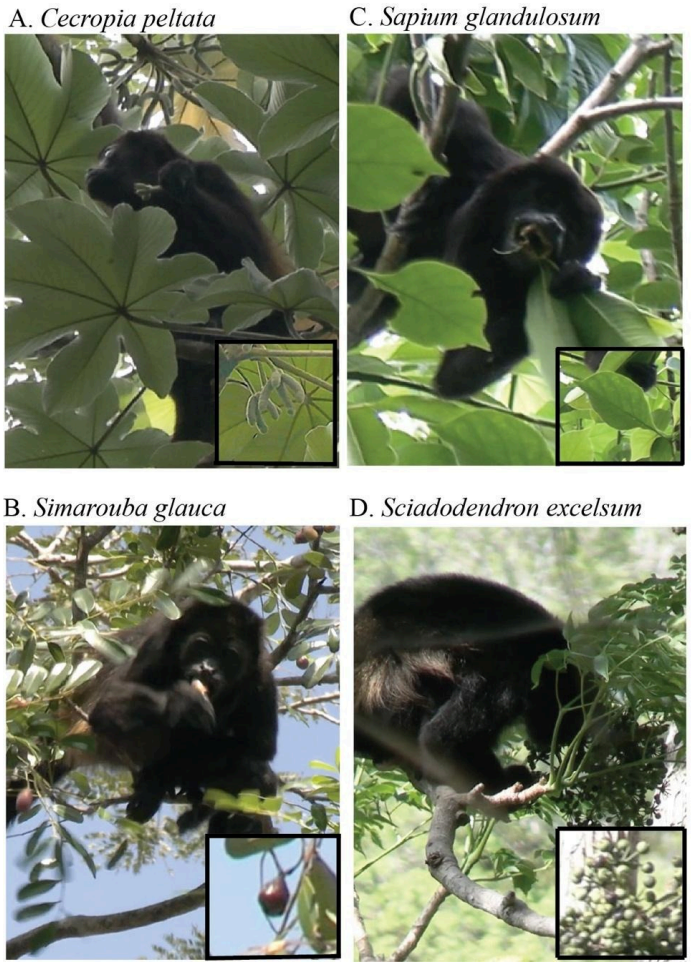
We observed 289 instances in which a howler monkey brought a hand to the mouth and adjusted the fruit or leaves in the mouth or made inhand-withdraw movements, in which they brough a food item, which was already held in hand, to the mouth.

The adjustment movements of a food item that was in the mouth (n = 140/289) were observed after a monkey had taken a bunch of leaves into its mouth with a branch-withdraw movement. A hand was used to push the leaves into the mouth.

Inhand-withdraw movements (149/289) occurred secondarily after a monkey brought a food item, that had been taken from the mouth, back to the mouth again. One of the 149 inhand-withdraw movement occurred when the branch that a monkey was pulling broke free when pulled. There were 9/149 instances inhand-withdraw associated with eating the fruit of *Cecropia peltata* (Berg et al. 2005). This fruit is also known as “gummy worm fruit” and features individual items of fruit growing in clusters from a single stem (Figure 4A). When a howler monkey grasped a stem, the cluster readily broke free into the monkey’s hand. The monkey then used inhand-withdraw movements to bring the cluster to the mouth and individually take each fruit item from it. The ease with which the stem of the fruit cluster broke from a branch suggested that these fruit-picking acts were not intentional discrete grasp-withdraw movements but rather were occasioned by the fruit breaking free from the branch when pulled.

Figure 4

Food Items Featuring Inhand-withdraw and Mouth-withdraw Movement



Note. A. The fruit of *Cecropia peltate*, when grasped, easily breaks from the stem leaving a cluster of fruit items inhand, which are then brough to the mouth with inhand-withdraw movements for eating. B. After obtaining the fruit *Simarouba glauca* by mouth with a branch-withdraw movement, a monkey takes the fruit from the mouth by hand and repeatedly makes inhand-withdraw movement to return the item to the mouth so the endocarp can be picked from the seed, which is discarded. C. The large leaves of *Sapium glandulosum* are picked using the incisors associated with a branch-withdraw movement. They are then taken from the mouth by hand, and the petioles are then presented to the molar teeth with an inhand-withdraw movement, to be bitten off for eating. The rest of the leaf is then discarded. D. The fruit *Sciadodendron excelsum* occurs in bunches on a thick branch and so are difficult to grasp by hand, resulting in a mouth-withdraw.

There were 135/149 inhand movements involving bringing the fruit of *Simarouba glauca* to the mouth (Figure 4B, Video S2). This is a plumb sized fruit containing a large seed (Manasi & Gaikwad, 2011). The fruit was picked by mouth from a branch in association with a branch-withdraw movement. A monkey then took the fruit from the mouth by hand and proceeded to process it by biting off pieces of pulp with repeated inhand-withdraw movements. Once most of pulp of the fruit was eaten, the seed was released by the hand and so dropped.

As is shown in Figure 4C (Video S3), 4/149 inhand-withdraw movements were made by a monkey eating the leaves of *Sapium glandulosum* (Andrade et al., 2017). The leaves of this plant are large and the howler monkey was observed to pull in a branch by hand and pull off some leaves with its incisors. Once the leaves were held in the mouth, they were taken from the mouth by hand. The monkey then oriented the leaves to present the pedicel of the leaf to the molars, and these were bitten off for consumption. The hand

then opened and dropped the rest of the leaf. Examination of the leaves of *Sapium glandulosum* indicated that they exuded a white latex when damaged. It is uncertain whether the latex is the target of petiole eating by the monkeys, but the latex is described as rich in protein and lipids (Rosa et al., 2024).

Mouth-Withdraw

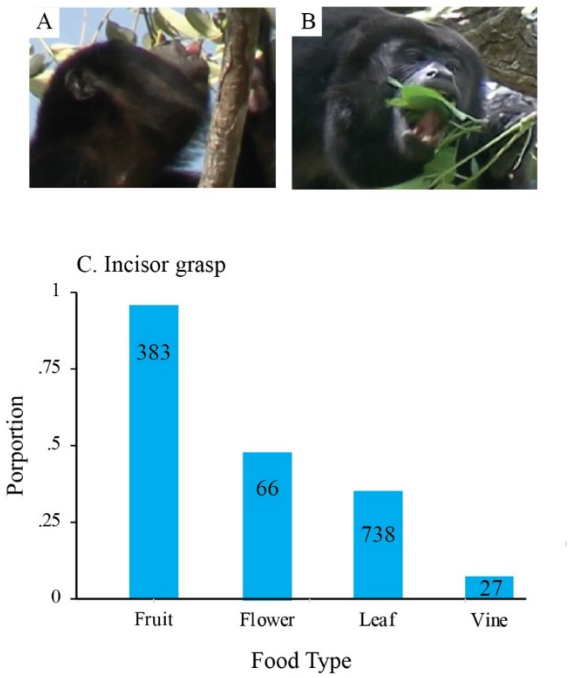
There were 10 instances in which a howler monkeys used a mouth-withdraw movement, in which only the mouth reached for a food item (Figure 4D). These instances of mouth-withdraw were associated with eating the fruit *Sciadodendron excelsum* (Chavarría et al., 1998). The fruit occurs in upward growing clusters attached to a relatively thick branch. The howler monkeys did attempt to grasp the branch, or attempted to grasp the fruit bunch itself, but apparently being unsuccessful, they then resorted to taking the fruit by mouth.

Incisor vs Molar Teeth Grasps

The incidence of taking a food item from a branch using the incisor teeth or the molar teeth is summarized in Figure 5. Figure 5A illustrates a howler monkey picking a *Simarouba glauca* fruit with its incisors. Figure 5B illustrates a howler monkey fully opening its mouth to grasp *Bursera simaruba* leaves using its molar teeth. Figure 5C illustrates the proportion of different food items (fruit, flower, leaf, vine) picked using the incisor teeth. The differential use of mouth grasps, in which fruit and flowers were picked largely using the incisors and leaves and vines were largely picked using the molars, was significant, $\chi^2(4) = 404.8$, $p < .001$.

Figure 5

Use of Incisor and Molar Teeth to Take Food Items from a Branch



Note. A. Example of a howler monkey picking the fruit *Simarouba glauca* from a branch using the incisor teeth. B. Example of a howler monkey picking the leaves of *Bursera simaruba* from a branch using a wide-open mouth and the molar teeth. C. The proportion of incisor grasps for fruits, flowers, leaves and vines. The numbers in each bar represent the total number of observations for that food type.

Arm and Head Contributions to Reaching

The relative contribution of the arm and head to reaching was scored on a 5-point scale with 0 indicating that the head only reached to take the food and 4 indicating that it was the hand only that brought the food to the mouth. Scores from 2208 branch-withdraw movements gave a mean score of 2.95±.01, indicating that hand movement accounted for most of the withdraw movement. The mouth only contributed by making orientation movements to grasp the item once it was brought proximate by hand.

The distance of the hand from the mouth, as an item was grasped from the branch by the mouth, was rated on a 3-point scale. Score-0 indicating that the hand was adjacent mouth, a score of 1 indicating that it was about a hand width distance away, and score-2 indicating that it was approximately the distance of the forearm away. The score (mean±sem = 0.05 ± 0.19), indicated that on 2208 withdraw movements the hand was usually adjacent to the mouth. Thus, this score indicated that a branch-withdraw was usually made by positioning the hand on the branch adjacent to a food item that was to be taken.

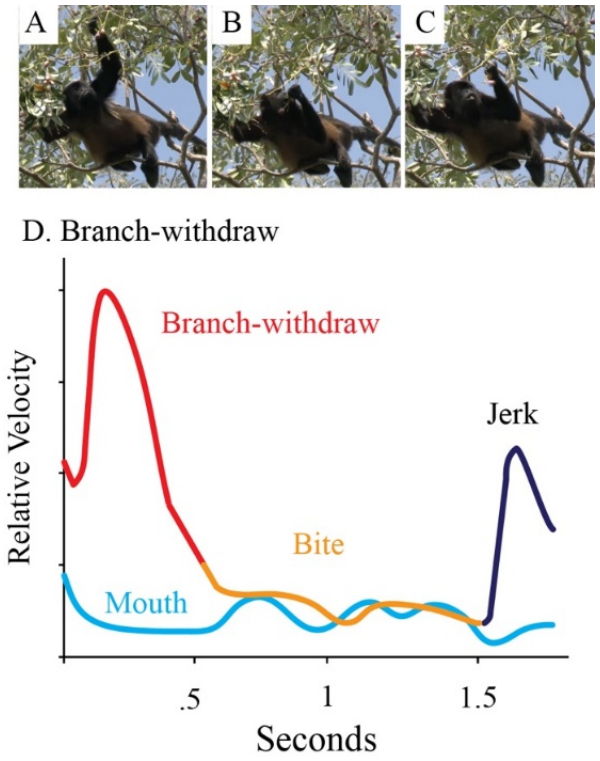
Food Items Removed from a Branch with a Jerk from Branch Recoil

Figure 6 (Video S4) illustrates the main features of a branch-withdraw movement from one reach in which all component movements were clearly visible. Figure 6A shows that the left hand reaches to grasp a branch at a point adjacent to a cluster of *Simarouba glauca* fruit. Figure 6B illustrates that as the hand is brought adjacent to the mouth, the mouth reaches and takes one fruit item in the incisors. Figure 6C illustrates that the fruit is jerked by recoil from the branch as the hand relaxes its pull, by lower arm extension, allowing the branch to jerk away leaving the food item in the mouth. All branch-withdraw movements that were observed featured a jerk to remove a food item. If a branch had minimal potential energy having not being bent when brought to the mouth, lower arm extension was still used to pull a target of eating free from the branch.

Figure 6D gives a kinematic representation of the head and hand movement (digitized on the knuckle of digit 5 and the tip of the nose) associated with the jerk act of picking a fruit item. The traces show that the picking act has a relatively high velocity movement for the hand when approaching and grasping the branch. There is a gradual decrease in velocity as the branch is brought toward the mouth. The kinematic trace representing the mouth shows that other than an orienting movement, the branch-withdraw movement involves little movement of the head. The mouth kinematic trace also shows that the monkey takes about a second to grasp a fruit item with the mouth. The kinematic trace of the hand shows that the fruit item is jerked from the branch by the hand relaxing its pull on the branch by lower arm extension allowing the branch to spring away. The jerk that picks the food item from the branch act is indicated by the increase in hand velocity at the point of the curve labeled as “release” (which is featured by a blur of the hand in Video S4).

Figure 6

A Branch-withdraw With a Jerk to Remove a Simarouba glauca Fruit



Note. A. The reach with the left hand grasps a branch containing *Simarouba glauca* fruit. B. The branch-withdraw brings the fruit to the mouth so that a fruit item can be grasped in the incisors. C. The jerk by which the fruit is pulled from the branch occurs when hand relaxes its pull on the branch with a lower arm extension movement. D. A kinematic representation of hand and mouth movements showing the velocity increase and decrease related to the reach and branch-withdraw, the relative absence of hand and mouth movements as the mouth grasps the fruit, and the jerk associated with the release of the pressure with which the branch was pulled, resulting in the fruit being pulled from the branch. Note that the mouth makes relatively little movement during the reach and jerk associated with taking the fruit. Movement digitized on the knuckle of digit 5 and the nose tip.

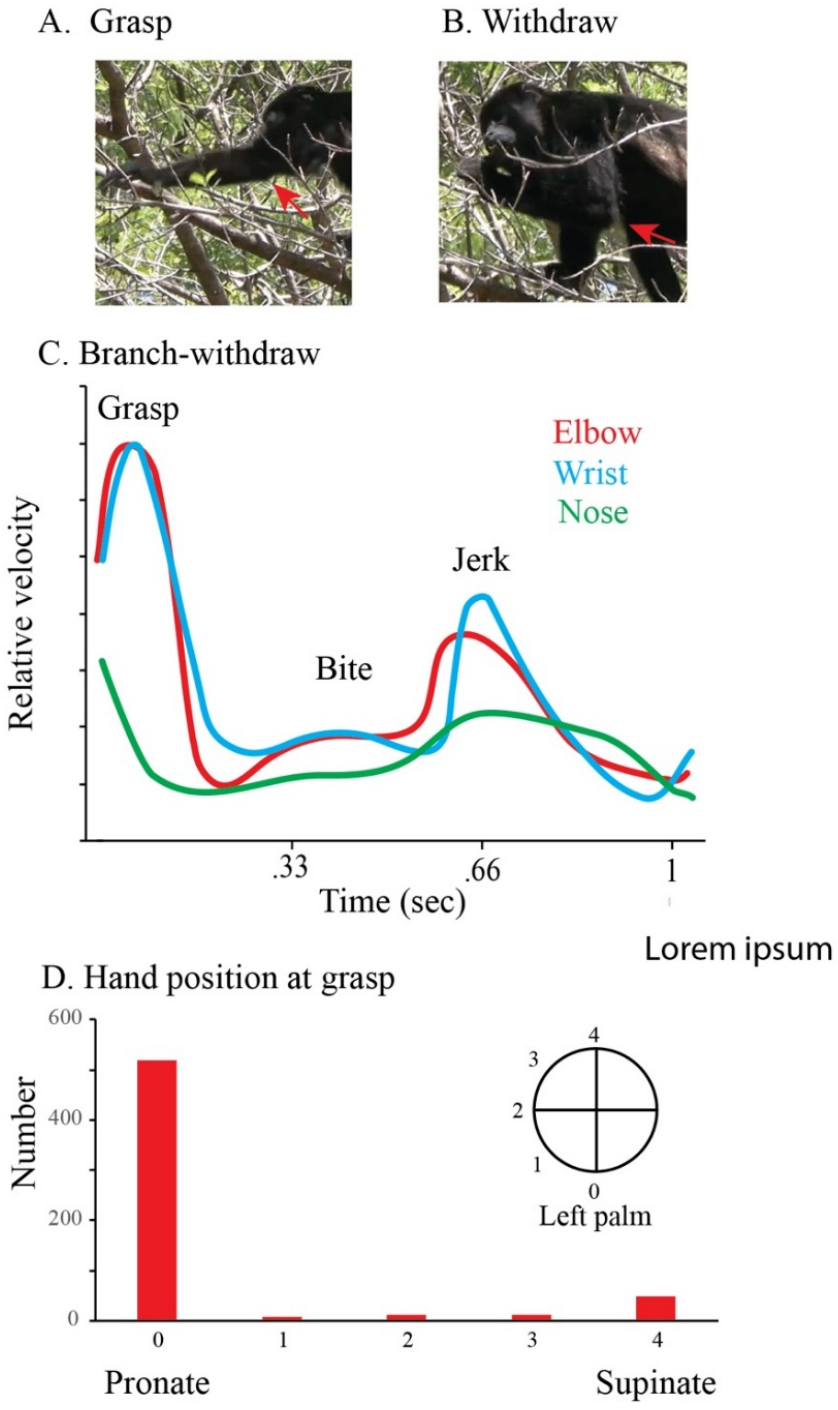
Upper Arm Used to Reach and Withdraw With Pronated Grasps

Arm movement and the grip were scored for 623 branch withdraw movements in which the acts were clearly visible. Figure 7 (Video S5) gives an example of the most frequently used movement (566/623 or 90.8% of observations), in which the upper arm (red arrow) carries the lower arm and hand to make the reach (Figure 7A) and the withdraw (Figure 7B). Of the remaining 38/623 observations, the reach and withdraw were made using a lower arm movement, in which the elbow was flexed to carry the hand to the mouth. Figure 7C give a kinematic representation of an upper arm branch-withdraw movement, in which elbow and the wrist are digitized. The synchrony of the movement of the elbow and wrist illustrates that most of the movement is obtained from upper arm movement. After the bite, the kinematic curves indicate that pull exerted on the branch is relaxed, thus jerking the fruit item free from the branch.

As summarized Figure 7D, when the hand grasped the branch, it was fully pronated on 519/623 (83.3%) occasions. On 48 (10.9%) occasions, the hand fully supinated to grasp. The remaining 56 observations had intermediate angles of orientation. Additionally, all withdraw movements carried the hand grasping the branch to a position at which the radial side of the hand was facing toward the mouth so that item on the branch could be grasped by the mouth. The use of lower arm flexion and hand supination for grasping occurred together (48/623 observations), mainly when a prospective food item was already relatively close to the mouth.

Figure 7

Grasp Posture and Upper Arm Movement Associated with a Branch-withdraw



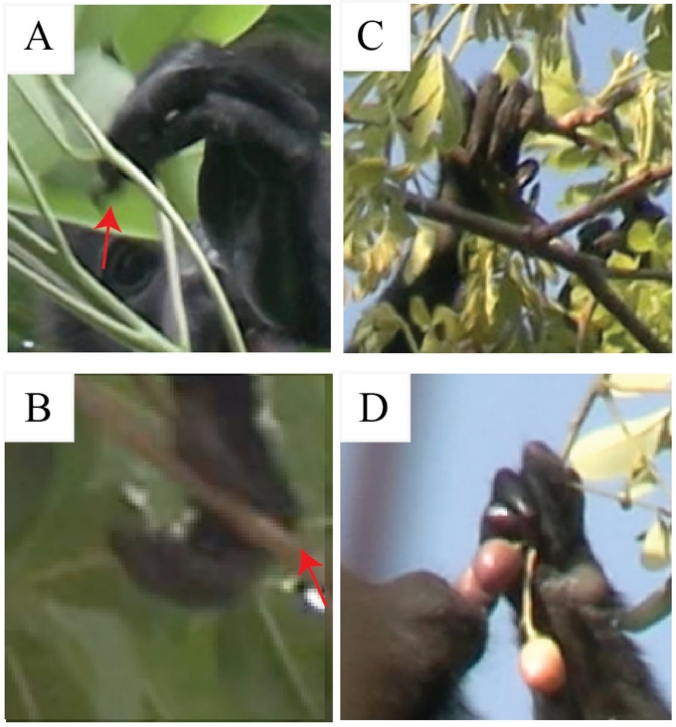
Note. A. The upper arm abducts, and the grasp of a branch is made with a pronated hand. B. The upper arm adducts to withdraw the branch toward the mouth to harvest a *Simarouba glauca* fruit with the incisors. C. Kinematic representation of the branch-withdraw, the bite, and the jerk to remove the leaf. Note the parallel velocity of the hand and elbow indicating the hand is carried by upper arm movement. D. The relative incident in hand position rated on a 5-point scale (0 = pronate, 4 = supinate) for grasping, in which most grasps are made with a pronated hand.

Hand Grasps

The way in which a hand grasps branches was scored from 688 grasps. For 670/688 or 97% of grasps, the fingers opened together and then closed together. First contact with a branch for power grasps could be made with any part of the ventral hand surface, from the distal part of the finger, as shown in Figure 8A, to the heel of the palm, as shown in Figure 8B. Once first contact was made, the finger might flex to hook and pull an item as shown in Figure 8C or fully close in a power grip and pull as shown in Figure 8D. Often hooking occurred first and then hand closing occurred as the branch was pulled toward the mouth. Only 12/688 grasps involved a zygodactylous (or schizodactylous) scissor grip as defined by Youlatos (1999). This grasp had a branch grasped with D1-2 on one side of the branch and D3-5 on the other side, which is the grip used by a howler monkey for grasping a branch with a hand when walking. On 6/688 grasps, finger closing involved D3-5 clamping the branch, which appeared to be a modified zygodactylous grasp, in which D1-2 were not closed. In all, a power grip and not a scissored grip was preferentially used for grasping.

Figure 8

First Hand Contact and Grasp Type for Branch-withdraw



Note. A. First contact (arrow) is made with the distal digits and a branch of *Bursera simaruba*. B. First contact is made with palmar surface (arrow) on a *Ficus goldmanii* branch. C. A branch-withdraw is made with the fingers hooked around the branch of *Samanea saman*. D. A branch-withdraw is made with a whole hand grip with the digits converged toward the hand midpoint to grasp a branch holding *Simarouba glauca* fruit

Discussion

Our analysis of 2208 reaching for food events shows that the feeding behavior of the howler monkey *Alouatta palliata* is an admixture of inverted positional behavior and a simplified reach to pull branches to take their fruit, flower, leaves or vines by mouth. Over one half of reaches were made with the assistance of tail-suspension, allowing almost equal above and below branch feeding access. Reaches

featured upper arm adduction and power grips made with a pronated hand, to grasp branches proximal to a target food item. The incisors were used to take fruit and flowers, and the molars were used to take leaves from a branch. Food was plucked from a branch by the recoil from relaxing the pull on the branch via lower arm extension. The howler monkeys made only a few discrete grasps in relation to positioning and adjusting food items at the mouth. The results suggest that howler monkey feeding is derived, featuring a reach specialization. This specialization supports dual visuomotor theory, which suggests that the reach and grasp can have separate evolutionary histories. This specialization may contribute to many howler monkey morphological features including a small brain and an energy minimizing lifestyle.

Howler monkeys have the shortest but heaviest tail of the atelid primates, with the longest hairless area (Youlatos et al., 2015). Their stocky tail and physique combined with an above-branch positional quadrupedal repertoire, has suggested that they may make less use of tail-suspensory feeding than for their more agile cousin *Ateles* (Ankel, 1972; Cant, 1986; Mittermeier van & Roosmalen 1981; Rosenberger & Strier, 1989; Youlatos et al., 2015; Youlatos, & Guillot, 2014). Our finding of a 57% incidence of tail suspension by howler monkeys, vs a 48% incidence for the spider monkey *Ateles geoffroyi* when studied in the same habitat using identical methods (Whishaw et al. 2025), shows that howler monkeys engage in extensive suspensory positional behavior, exceeding that of spider monkeys. Tail suspension may optimise food access both above and below a supporting branch location, especially with respect to access to leaves, and so minimize travel associated with moving between foraging patches. The howler monkeys use of tail suspension suggests that this is a conserved behavior in the family Atelidae for local movement.

There have been anecdotal descriptions of howler monkey hand use for natural foraging, with the conclusion that their hand skills are crude, even resulting in the dropping of a third of the food that they pick (Carpenter, 1934; Smith, 1977; Ungar, 1990). Our findings show that their hand use is specialized for branch reaches. They use an upper arm movement to reach for and withdraw branches that they grasp with a pronated power grip. They can occasionally use a supinated hand and lower arm flexion to withdraw branches for food items that are close to the mouth. Independent hand use was sparingly used to handle fruit and leaves already taken by mouth, including the fruit of *Simarouba glauca* and the leaves of *Sapium glandulosum*. They used a hand to reposition these foods for selective biting, discarding unwanted portions. The use of a relatively simple reach to bring branches to the mouth combined with more independent hand movements around the mouth is perhaps not surprising. Many animal species, that do not guide their hand with vision when reaching will harvest food by mouth and then, squirrel-like, will take those food items from the mouth by hand for further handling when eating (Iwaniuk & Whishaw, 2000a; Sustaita et al., 2013; Whishaw & Karl, 2019). Taken together, the present observations support the view that the howler monkeys display a derived reach strategy. Nevertheless, they make efficient use of their hands and dropping food may represents not waste but perhaps a disposition to be picky eaters.

When howler monkeys walk along branches, the hands use a zygodactylous grip in which D1-2 and D3-5 clasp a branch (Youlatos, 1999). The present observations show that they seldom use a zygodactylous grip to pull branches. Their branch grasps were made mainly with power grips, with a target grasped between D2-5 and the palm (Naper, 1956; 1962). In making power grasps, first contact with the hand on a branch appeared to be made with the palmer surface, anywhere from the distal phalanges to the palm heel, with the fingers then closing with the assistance of wrist flexion. Although howler monkeys are not considered skilled in making food handling movements (Baum, 2005), their power-grip for branch handling movements are complex in that they feature a variety of contact and power grip variations (see Figure 8D). Filming in the present study included the entire monkey, which prevented more detailed focus on the hands. Close-up filming of the hands could be done in future studies to better describe the role of thumb and fingers in branch manipulation.

The almost exclusive use of a reach strategy by howler monkeys lends support to dual visuomotor theory, which suggests that reaching is a composite of the reach and the grasp, each of which can have independent evolutionary histories (Grant & Conway, 2019; Goodale et al., 1994; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Karl & Whishaw, 2013; Hoff & Arbib, 1993; Marzke, 1971; Nashner & McCollum, 1985; Sartori et al., 2015; Whishaw et al., 2019, 2025). The reach strategy of howler monkeys represents an extreme reach specialization that almost eliminates a role for an independent grasp by the

mouth and hands. This specialization likely provides a competitive feeding niche in relation to sympatric capuchin and spider monkeys while additionally enabling the occupancy of marginal habitats (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Mittermeier & Roosmalen,1981; Youlatos et al, 2015). In short, we suggest that just as a stocky morphology of the forelimb can be selected for in howler monkeys (Youlatos et al., 2015), the neural substrates that enable a forelimb reach as a main strategy for feeding can be similarly selected.

The utility of the howler monkey's strategy of tail suspension and grasping branches and pulling them toward the mouth to harvest their content may contribute to their described energy minimization (Cortés-Ortiz et al, 2003; Di Fiore and Saurez, 2007; Fortes et al, 2014; Youlatos et al, 2015). Howler monkeys exclusive branch-reach behavior, in contrast to the more sparing use of this behavior by capuchins and spider monkeys (Whishaw et al 2025; 2026), may simplify movements of the hand, mouth, head and body. For example, by not using a hand to pick food from a branch, carry the food to the mouth, position the food for the mouth and then release it to the mouth, skilled movement components are reduced in a feeding repertoire. In addition, holding a branch enables many food items to be taken sequentially by mouth, which may represent an efficiency over making independent reaches for each food item. Moreover, as food is brought to the mouth, movements of the head and body are additionally minimized. A branch-pulling strategy may be especially useful for eating leaf clusters, allowing them to be harvested without numerous sequential reach and grasp movements. The putative simplification of eating movements resulting from branch withdraws, combined with enhanced food accessibility, could be examined in laboratory studies to confirm that they are strategies that reduce energy use.

The howler monkey branch reaching behavior may contribute to distinctive features of its nervous system. *Alouatta palliata* has a brain that is one half the size of its similarly sized relative *Ateles geofforyi*, a difference that Milton (1993) attributes to being a folivore vs frugivore. Although there is an ongoing debate about the relationship between brain size and hand skills (Iwaniuk et al., 1999; 2000b), it is also suggested that the commitment of sensory systems - and especially vision - to reach and grasp control may influence brain size (Baker et al., 2025; Sobinov & Bensmaia, 2021; Whishaw, 2003). The reduction in the use of grasping by *Alouatta palliata*, with a concomitant reduced need for touch and vision for skilled hand movement for food grasping, may reduce the need for complexity of brain networks to mediate oromanual behavior (An et al., 2022). Network simplification may in turn contribute to reduced brain size. In this respect, it is interesting that Sfar et al., (2014) report that none of 12 howler monkeys could perform two hand-related laboratory tasks that 7 capuchin monkeys performed with ease. Possibly, reduced hand skill in natural foraging and presumptive brain changes have consequences for skilled behavior involving the hands more generally.

The reach strategy of howler monkeys may influence other morphological characteristics, including dentition, visual ability, arm structure and locomotion. With respect to dentition, *Alouatta* is described as molar centric, with large molars designed for leaf chewing. Its incisors are also special in being blunt and tapered mediolaterally, seemingly designed for biting and pulling (Ungar, 1990; Anapol & Lee, 1994). Here, we found that the monkeys use their incisors for holding onto food items as they were jerked from branches. Possibly, such pulling could break thinner, unspecialized incisors. It is recognized that *Alouatta palliata* is distinctive among platyrrhine primates in having routine trichromatic vision (all individuals have red-green color vision), which is proposed to be useful for ripe fruit and young leaf selection (Dominy & Lucas, 2001; Kainz et al., 1998; Melin et al., 2017; 2022). Their unique feeding niche, and the instances of picky behavior noted here in selecting leaves and fruit, is likely aided by trichromatic vision as suggested by Melin et al., (2017; 2022). *Alouatta* also has an unusual fovea and visual cortex. It has a higher peak cone density in the foveal pit, than is observed for other diurnal monkeys (Franco et al., 2000) and has sharply delineated ocular dominance columns in visual cortex, an unusual feature in platyrrhine primates (Florence et al., 1986). Here we observe that when howler monkeys pull in a branch, inspect it, and use their mouth to pick its leaves or fruit, their selection for mouth grasping is made at close quarters to the target, suggesting that they may have a short visual fixation distance. This might be enabled by their foveal and visual cortex features permitting a high chromatic acuity in a restricted central region (Muniz et al, 2014). In their review of the forelimb of *Alouatta*, Youlatos et al., (2015) note that it is short and stout,

suggestive of a restrictive emphasis on abduction and adduction movements and weight bearing optimal for quadrupedal walking. Possibly, these forelimb features are partly derived from the howler monkey branch-withdraw feeding strategy that mainly relies on upper arm abduction and adduction movement.

In summary, we have made a video-based analysis of the natural foraging and food picking behavior of *Alouatta palliata*. We find that the howler monkeys feature a specialized branch reach foraging strategy that is integrated with tail prehension enabled positional behavior. Our observations contribute to the evidence that there is a broad variation in the feeding abilities of platyrrhine primates. Variety ranges from grasp-centered reaching of *Cebus imitator*, akin to that of catarrhine primates, to a reach-centered reaching of *Alouatta palliata*, that is even more simplified than that of strepsirrhine primates, which also use a mainly reach strategy. Our results support the theory that reaching is a composite of reach and grasp movements that can be subject to evolutionary selection. Our results also contribute to the view that specialization in a reach strategy may contribute to other *Alouatta* behavioral and morphological features that enable an energy minimizing lifestyle. It would be interesting to extend the reaching analysis used in the present study to the natural foraging behavior of other primates in the family Atelidae, e.g. *Brachyteles* and *Lagothrix* genera, as well as to the many other species of platyrrhine primates. Such comparisons could contribute to understanding the genetic and neural processes that enable the striking variation of reaching skills in these monkeys, results that could have a bearing on understanding the evolution of hand use in primates more generally.

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Data Availability: See Supplemental materials for links to referenced videos.

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Supplementary Materials

Video S1.

Branch-withdraw.

https://doi.org/10.6084/m9.figshare.32983391

Note. A branch-withdraw by juvenile female howler monkey in which she pulls by hand a *Foresteronia spicata* vine toward her mouth. She bites a portion of the vine and an attached leaf that is located proximal to her right hand. The molar teeth are used to bite. When the pull on the branch is released, it jerks the target food off the branch. The monkey is in an inclined position (position 1), supporting herself with her tail and hind feet. 10% video speed.

Video S2.

Inhand-withdraw of Simarouba glauca Fruit.

https://doi.org/10.6084/m9.figshare.32983553

Note. A female howler monkey with and infant uses the left hand to make a branch-withdraw, so that the right hand can then also take the branch near the targer fruit item. The monkey picks a *Simarouba glauca* fruit item using the incisor teeth from the branch held by the right hand. Once the monkey has the fruit in its incisors, it takes the fruit from the mouth using a precision-power grasp, which holds the fruit against the palm on the radial side of its right hand with its digit tips. It then makes an inhand-withdraw to return the fruit back to the mouth to chew the exocarp from the fruit. 10% video speed.

Video S3.

Inhand-withdraw of Leaves and Petiole Removal

https://doi.org/10.6084/m9.figshare.32983691

Note. An adult male howler monkey makes a branch-withdraw of *Sapium glandulosum* leaves by grasping the petioles of a few leaves with its molar teeth. The monkey then reaches with its left hand to remove the leaves from its mouth and reorient them to place the petioles across its molar teeth. It bites off the petioles for consumption and then discards the leaves. The monkey is in an inclined position (position 1), supporting himself with his tail and hind feet. 10% video speed.

Video S4.

Jerk to Obtain Fruit with Branch Pull Jerk

https://doi.org/10.6084/m9.figshare.32983808

Note. A female howler monkey makes a left-hand branch-withdraw of a branch of *Simarouba glauca* to take one fruit item in its incisors. By releasing pressure on the pull of the branch, by extending the lower arm, the fruit is jerked from the branch to be left between the incisors. The blur of the hand, as the pull on the branch is relaxed, indicates the jerk. The monkey is in an inclined position (position 1), supporting herself with her tail and hind feet.10% video speed.

Video S5.

Abduction and Adduction Using the Upper Arm to Make a Branch-withdraw

https://doi.org/10.6084/m9.figshare.32983820

Note. An adult female howler monkey makes a branch-withdraw using left upper arm abduction to reach to grasp the branch with a pronated hand, followed by upper arm adduction, to withdraw a branch that she been grasped. The monkey is in a horizontal position (position 0), supporting herself with her tail and hind feet.10% video speed.