The Platyrrhine Primate *Cebus imitator* Uses Gaze to Manipulate and Withdraw Food to the Mouth

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Abstract – Orienting a food item held in the hand to withdraw and optimally place it in the mouth for eating (withdraw-to-eat) is mediated by vision in catarrhine anthropoids and by nonvisual strategies in strepsirrhine primates. The present study asks whether vision contributes to the withdraw-to-eat movements in a platyrrhine anthropoid *Cebus imitator*, a member of a monophyletic primate suborder whose stem group diverged from catarrhines about 40 million years ago. *Cebus imitator's* gaze and hand use for foraging for fruit is examined in its fine branch niche, the terminal branches of trees. Video of reach, grasp and withdraw-to-eat movements with associated gaze were examined frame-by-frame to assess food manipulation and its sensory control. *Cebus imitator* uses vision and touch to reach for and grasp food items with precision and whole hand grasps. They use vision to orient food items held in-hand into a precision grip and their withdraw-to-eat is assisted with a vertically oriented hand. The conjoint use of vision, a precision grasp, and hand posture and a central representation of object control likely originated in stem anthropoids and was derived from the staged evolution of the visual manipulation of food and other objects.

Keywords – Capuchin feeding, Food manipulation, Fruit foraging, Primate hand use, Vision for hand use, Visual food handling, Platyrrhine primates

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The evolutionary origins of the visual control of reaching for eating, tool use, and other skilled hand activities by humans is unresolved. In addition, contemporary visuomotor channel theory proposes that skilled forelimb use is composed of a number of sub movements; for example, the reach, the grasp, and the withdraw of a food item to the mouth (Grant & Conway, 2019; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Sartori et al., 2015; Whishaw et al., 2016). This organization implies that each channel and subcomponent movement has its own evolutionary history (Karl & Whishaw, 2013). Insight into the visual control of hand use related to the sub movements of reaching can be obtained by examining these movement in the many animal species that use their hands for food manipulation (Iwaniuk et al., 1998; Iwaniuk & Whishaw, 2000; Sustaita et al., 2013; Whishaw & Karl, 2014, 2019), especially extant primates that use vison for food manipulation. Catarrhine primates—as represented by macaques (*Macaca*), anthropoid members of the subfamily Cercopithecinae—pick up food items using hand and finger shaping strategies that include pincer and precision grasps. These grasps are appropriate to the size and shape of food items (Bishop, 1964; Christel, 1993; Christel & Fragaszy, 2000; Macfarlane & Graziano, 2009; Marzke et al.,

2015; Pouydebat et al., 2008; Scott, 2019). Cercopithecinae primates also visually examine food objects that they hold in the hand and use vision to orient those food items prior to withdraw-to-eat, as do other catarrhine anthropoids including humans (Hirsche et al., 2022). The co-occurrence of visually controlled precision grasping and visually controlled food manipulation in-hand for withdraw-to-eat in catarrhines suggests that the visual control of these behaviors may be related. Comparative studies support this conclusion, as nonprimate species do not use visually mediated hand shaping for reaching or for oromanual behaviors such handling food items for placement in the mouth. Nonprimate species pick up a food item by mouth and/or reach with the mouth to take a food item held in the hand (Ivanco et al., 1996; Iwaniuk et al., 1998; Sustaita et al., 2013; Whishaw & Coles, 1996; Whishaw et al., 1998, 2018, 2020). Strepsirrhines, an early branching suborder of primates, also do not make visually mediated hand shaping movements for picking up food or for food handling during withdraw-to-eat (Reghem et al., 2011, 2013; Perrenoud et al., 2020; Pouydebat et al., 2008, 2009). Some strepsirrhine species may visualize and pick up smaller food items by mouth (Peckre et al., 2019) and all strepsirrhine species use their mouth to take food from the hand and use nonvisual strategies for hand to mouth food transfer (Peckre et al., 2023).

The use of vision for object grasping and for in-hand withdraw-to-eat movements to place food into the mouth in catarrhines, *versus* the absence of similar visual use in strepsirrhines, raises questions related to the evolutionary origins of the visual contribution to these visually mediated movements. Did visual control of the grasp and the withdraw-to-eat movement coevolve, did visual control of the grasp contribute to the subsequent visual control of the withdraw-to-eat movement, or was this sequence of events reversed? Evidence related to these questions could be obtained by examining the sensory control of the grasp and the in-hand withdraw-to-eat movement in the other major radiation of anthropoids, the Platyrrhini of the Americas. The stem group of this monophyletic primate suborder split from catarrhines about 40 million years ago (Arnold et al., 2010; Kay et al., 1997; Kissling et al., 2015), and so the strategies that they use in feeding could provide insights into the evolution of visually mediated reaching and withdraw-to-eat movements that are absent in strepsirrhines but present in catarrhines. Additionally, examination of the feeding behavior of platyrrhines might shed light on whether the acquisition of these behaviors was a singular event or whether one preceded the other. Thus, the objective of the present study is to determine whether a platyrrhine primate uses vision to orient food items held in the hand for placement in the mouth. The answer to this question is relevant to understanding the use of vision in object control by the hand more generally.

We studied a population of white-faced capuchins, *Cebus imitator,* from Costa Rica, members of the subfamily Cebinae. Among platyrrhines, Cebinae are described as especially skillful in hand use (Christel & Fragazy, 2000; Costello & Fragazy, 1988; Melin et al., 2022; Spinozzi et al., 2004; Truppa et al., 2019, 2021). They are also representative of a species foraging in a fine branch niche, a niche proposed to be central to the evolution of the visual control of hand (Cartmill, 1972, 1974, 1992, 2012; Sussman & Raven, 1978; Sussman, 1991; Sussman et al., 2013; Scott, 2019). Wild, unprovisioned *Cebus imitator* were filmed as they foraged in trees for a variety of fruits. The videos were trimmed to include examples of fruit picking and eating and were then examined frame-by-frame to assess gaze in relation to the reach, grasp and the handling/withdraw movements of bringing food items to the mouth using previously described methods (Hirsche et al., 2022; Peckre et al., 2023).

Materials and 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), and by Mercer University's Institutional Animal Care and Use Committee (A2002003).

Study Population

The feeding behavior of *Cebus imitator* was filmed in the Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10°450–11°000 N, 85°300–85°450 W). The study population consisted of 16 animals, five adult males, three adult females, two subadult males, three juvenile females, and three juvenile males. The animals appeared to be in good health and featured no disabilities that would interfere with food grasping or feeding. Filming consisted of short (<1–10 min) continuous video samples following a published protocol with strict out-of-site rules, such that recording of behavior was done when there was a relatively unobstructed view of the focal monkey's feeding behavior (Melin et al., 2022). Individuals were sampled opportunistically, based on visibility, but observations rotated among sex and age classes to sample evenly across the population. The identity of every subject in a film clip was difficult to determine, but because no obvious behavioral differences were observed between identified subjects, the population was treated as a single group.

Video Recording

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

Food Items

Fruit items eaten by the capuchins included *Bromelia pinguin* (wild pineapple, Piñuela; round, 3-4 cm), *Spondias mombin* (hog plum, Jocote jobo; ovoid, 3.5-5 cm long, 2.5-3 cm wide), *Bursera simaruba* (gumbo-limbo, Indio desnudo; round, 1-1.5 cm), *Trichilia martiana* (Manteco; round, 1-1.5 cm), *Genipa americana* (Guaitil; round, 6-8 cm)**,** *Diospyros salicifolia* (persimmons, Lorito; round, 1.5-2 cm), *Byrsonima crassifolia* (nance; round, 1-1.5 cm), *Luehea candida (*Guácimo molenillo; ovoid, 6-8 cm long, 3.5-5 cm wide), *Ficus cotinifolia (fig,* Higuerón; round, 1-1.5 cm), *Ficus ovalis* (fig*,* Higuerón; round, 1-1.5 cm), *Ficus hondurensis* (fig, Higuerón; round, 1-1.5 cm), and *Stemmadenia obovata* (Huevos de burro; ovoid, 6-7 cm long, 3-4 cm wide).

Behavioral Analysis

Video Analysis

The video recordings of capuchin eating were examined frame-by-frame using Quicktime 7.7 software on an Apple computer. IQW performed the behavioral scoring, detailed below, based on previously described methods (Hirsche et al., 2022; Peckre et al., 2023). The scoring systems obtained from frame-by-frame video analyses have yielded an inter-scorer reliability coefficient of 0.96, based upon randomly selected videos representing a sample of approximately 10% of the video cuts (Hallgren, 2012). Every feeding sequence, in which a capuchin reaches for, grasps, withdraws and places a food item in the mouth was analyzed. Because animals were reaching through leaves and adjusting posture, some component movements of a reach were visible and others were obscured. Nevertheless, the observable components were always scored.

Behavioral Analysis

Body posture. Body posture associated with reaching movements was scored on a 5-point scale (following Laird et al., 2022; Peckre et al., 2023) using an Eshkol-Wachman numeric system (Golani, 1994):

- 0 – A score of "0" was given if the long axis of an animal's body was in a horizontal orientation relative to the relative to the substrate on which it was positioned.
- 1 – A score of "1" was given if the torso was in about a 45° upright orientation from the horizontal.
- 2 - A score of "2" was given if the long axis of an animal's body was in a vertical upward orientation relative to the food target for which it was reaching.
- -1 – A score of "-1" was given if the torso was in about a 45° downward orientation from the horizontal.
- -2 - A score of "-2" was given if the long axis of an animal's body was in a vertical downward orientation relative to the food target for which it was reaching.

Stance. Stance was scored on a 5-point scale in relation to the number of limbs that were supporting the body during a reach for food and withdraw of the food (Reghem et al., 2011; Whishaw et al., 1998). Although the tail contributes to support, it was not included in the stance score:
- 0 – designated that an animal was draped over a branch or suspended by the tail.
- 1 – designated that an animal was standing on one limb.
- 2 – designated that an animal was supported on two limbs, usually in a sit posture.
- 3 – designated that an animal was supported on three limbs, usually reaching with the fourth limb.
- 4 – designated that an animal was supported on four limbs and was thus reaching with its mouth.

Head orientation. The extent to which the head contributed to the withdraw-to-eat movement of food by reaching for a food item was rated on a 5-point scale (Hirsche et al., 2022; Peckre et al., 2023):
- 0 – the head was advanced to the food and the food was grasped with the mouth
- 1 – the nose was placed near the target as the item was grasped by hand and brought to the mouth
- 2 – the hand and the mouth were brought toward each other such that the withdraw-to-eat movement was accomplished equally by the hand and mouth.
- 3 – most of the withdraw-to-eat was accomplished with the hand with only a small orienting movement made by the head toward the hand.
- 4 – the head was not advanced toward the food or withdrew as the hand brought the food toward the mouth.

Hand use for reaching. Two types of hand use for reaching were documented by counts of occurrences (Fragaszy, 1998; Spinozzi et al., 2004; Truppa et al., 2019):
- *Single hand use*: single hand use involved a capuchin advancing only one hand to grasp an item with the other hand used for either supporting weight or grasping a branch for balance.
- *Bilateral hand use*: Bilateral hand use involved a capuchin using one hand to grasp a branch containing a fruit item and manipulating the branch into a position from which the other hand could grasp the fruit on the branch.

Mouth grasping from the hand. The way in which the mouth grasped food items from the hand was documented with counts of occurrences (Hirsche et al., 2022):
- *Incisor grasp*: incisor grasp consisted of the mouth opening and grasping a food item with a precise grasp using the incisor teeth, usually with the food item presented to the front of the mouth.
- *Premolar grasp*: premolar grasps consisted of the food item being grasped by the premolar teeth, usually with the food item presented to the side of the mouth.

Adjunct oral movements. Associated with reaching behavior, the capuchins made two kinds of oral movements during reaching and these were documented in animals eating *Ficus ovalis*, a grape sized fig (Vainio et al., 2019):

- *Gapes*: gapes were mouth openings in which neither the tongue nor teeth other than the canines were visible
- *Spits*: spits involved an animal opening its mouth and spitting out food

Reaching/withdraw movements. A reaching movement consisted of advancing a hand to a food item, grasping the item, and withdrawing the food item to the mouth so that it could be grasped by the mouth. The component movements of a reaching movement were scored as follows (Karl & Whishaw, 2013):

- *Reach.* A reach consisted of an advance of the hand to a food item, and its duration was measured by counting video frames that started with the first movement of advancing the hand toward the food and ended with the frame on which the advancing movement ended.
- *Grasp.* A grasp consisted of shaping and closing the digits so that the food item was held in the hand, and each grasp was measured by counting frames, beginning with the last frame of the reach to the first frame where hand completed the grasp and moved toward the mouth.
- *Immediate Withdraw-to-eat.* An immediate withdraw-to-eat movement was a movement that brought a food item to the mouth without a pause after it was grasped, and was measured by counting video frames, beginning with the frame where the grasp ended to the frame at which the hand stopped to transfer the food item to the mouth.
- *One-handed food holding.* A one-handed food holding movement consisted of holding a food item in one hand before bringing the food item to the mouth.
- *Two-handed food holding.* A two-handed food holding movement consisted of holding a food item with both hands before bringing it to the mouth.
- *In-hand withdraw-to-eat.* An in-hand withdraw-to-eat movement consisted of bringing a food item that been held in one or both hands to the mouth. The duration of an in-hand withdraw-to-eat was measured by counting frames, beginning with the first movement of the hand holding a food item toward the mouth until the hand came to a stop to place the food in the mouth.

Hand grasps. The capuchins made different types of hand grasps when initially grasping and handling food items (for descriptions of capuchin hand grasps see Christel & Fragaszy, 2000; Fragaszy, 1998, Truppa et al., 2019). Hand posture was recorded both when a food item was picked up and when a food item was transferred to the mouth. Grasps were divided into two categories:

- *Cebus Precision grasp*: a food item was grasped or held mainly between the first two fingers (pollex and index finger) and might also be pressed against the palm. Although grasping using a digit pad and the palm is usually classified as a whole hand grasp, here use of the term precision grasp for capuchin grasping with the pollex and palm was both difficult to distinguish from grasps made between digit 1 and digit 2. This grasp also appeared to be sufficiently distinctive to receive the distinction of a *Cebus* precision grasp.
- *Whole hand grasp*: a food item was grasped or held between a number of digits and the palm.

Gaze. When food was grasped, if the head of an animal was oriented toward the food at the time that the grasp occurred, that was taken as a sign that the animal was looking at the food (i.e., visually engaged or gaze anchoring, as defined by Posner et al., (1987). The following head/eye orienting behaviors were quantified by counts of incidence and measures of duration by frame counting:

- *Engage*: a movement that resulted in the face/eyes being directed toward the food item before or as it was grasped.

- *Gaze anchoring*. Gaze anchoring, or duration, was measured with frame counts from the point that the head/eyes were directed to a food item to the frame on which they began to move away from that orientation, or the capuchin blinked.
- *Disengage*: a movement that resulted in the face/eyes being directed away from the food item that had been grasped (cf. de Bruin et al, 2008).
- *Eye blink*: Eye blinks were rapid closing and opening of the eyelid. The occurrence of a blink was noted for those video recordings for which a view of the eyes was adequate and as a proportion of all withdraw-to-eat movements (*cf*. de Bruin et al., 2008).

Measures of Duration. The contribution of gaze to the grasp and manipulation of a fruit item was assessed by counting video frames (30 fps) in order to derive measurements in seconds.

- *Reach duration.* Video frames measured wrist movement from the first frame on which a hand began its forward motion toward the target to the first frame in which movement was reversed.
- *Withdraw duration*. Video frames were counted during wrist movement from the first frame on which it began its withdraw motion toward the mouth to frame in which movement stopped as the hand reached the mouth.
- *Gaze duration*. Gaze associated with reach, food handling, and withdraw movements (also see above) was measured by frame counts during which the head was oriented to a food item for which a hand reached, withdrew and handled food, to the point that gaze was disengaged by a head movement away from the food item or by a blink.

Statistical Analyses

Counts of behaviors including posture, grasping type, engage and disengage, blinking and eye direction are reported as the percent of the number of observations that were made. The relationship between the duration of the immediate withdraw-to-eat and in-hand withdraw-to-eat movements to head-engage, eye engage, and disengage duration were assessed using the Pearson product-moment correlation and compared with Chi-square tests.
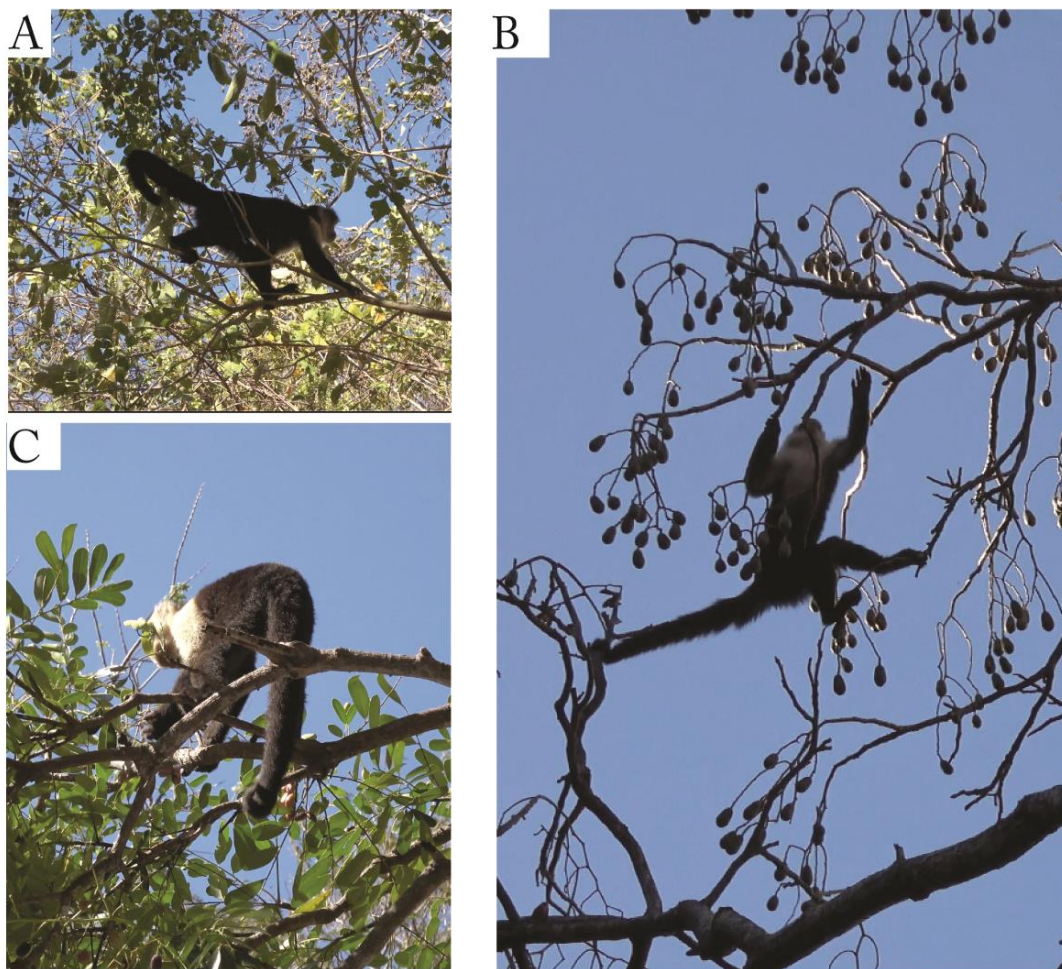
Results

The results were obtained from 390 video clips each ranging from 15 s to 10 min, and which together comprised 9.44 hr of video. Frame-by-frame inspection of the video provided 598 instances of reaching in which a movement sequence comprised a reach by hand for a food item, a grasp of the food item, and the withdraw of the food item to the mouth for eating. The capuchins were adept in moving on the terminal branches of trees and supporting themselves with various limb and prehensile tail configurations, all the while reaching, grasping, and withdrawing fruit items to the mouth for eating (Figure 1). Feeding principally occurred in the terminal branches of trees, a location described as a fine branch niche (Cartmill, 1972, 1974, 1992, 2012; Sussman, 1991; Scott, 2019; Sussman & Raven, 1978; Sussman et al., 2013). A few instances of animals coming briefly to the ground to pick up food items were observed, but the animals quickly returned to a tree to eat, consistent with the arboreal proclivities of this species (Fragaszy et al., 2004). When a part of the animal was hidden from view by branches or leaves, those parts of the reaching act that were visible are nevertheless described. Consequently, the following descriptions include different number of observations depending upon the component movement observed. Some of the animals' feeding movements differed depending upon the fruit and size of items it was eating, and these examples are described as a subset of reaching observations. Given that the data are obtained from the spontaneous behavior of the animals in trees, the movements of reaching were associated with a variety of body movements. Body movements were related not only to the movement of the animals themselves but also to the movements of the branches produced by the animal's postural changes, the wind, and movements

of other animals. Because the kinematics of reaching were not being measured, behavioral observations could be scored despite the complexity of substrate/body movements. The measures of reaching described below all involved reaching acts for obtaining food and bringing it to the mouth for eating. Reaching acts associated with bringing a food item to the nose for sniffing, grasping a food item and not picking it, and grasping objects that were released or dropped were not documented.

Figure 1

Foraging Habitat

Note. Capuchins foraging in: A. *Ficus cotinifolia*; B. *Cedrela odorata*; C. *Simarouba glauca*. Foraging involved moving amongst relatively small distal branches of trees, in what is termed a fine branch niche.

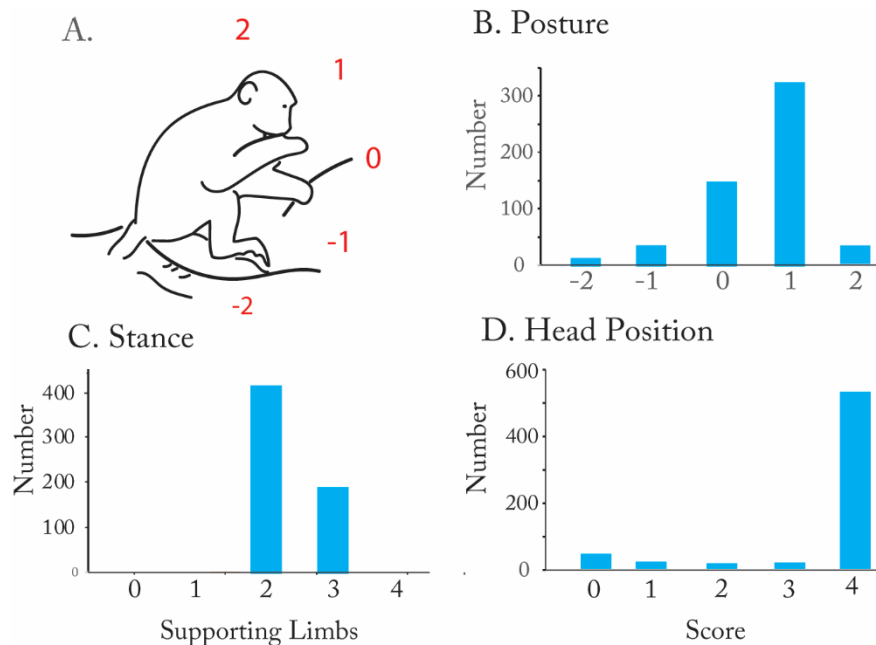## Favored Reaching Posture, Stance, and Head Orientation

The body posture, stance, and head orientations observed in 598 reaching observations are summarized in Figure 2. The most frequently occurring postural configurations associated with *Cebus imitator* reaching is shown in Figure 2A. This posture features the long axis of the body in an oblique orientation, stance is sitting on the haunches supported by the hind limbs, and the withdraw-to-eat movement is made by a single hand bringing a food item to the mouth. The numerical notation used to define posture is depicted by the numbers to the right of the cartoon capuchin (Golani, 1994; Pessina et al., 2019). Figure 2B illustrates the frequency of eating posture as designated by the numerical notations for

orientation shown in Figure 2A. Less frequently used postures included the body in a horizontal position and in a vertical position with the head up or down.

Figure 2

Postural Features of Capuchins When Consuming Fruit

Note. A. An illustration summarizes average postural features with an animal: sitting on its haunches with a trunk angle of approximately 45˚, supporting itself on two hind limbs, bringing a food item to the mouth with one hand, with the head upright and drawing away from a hand bringing food to the mouth (numbers refer to body angle, 0=horizontal, 1=angle of 45˚, 2+upright angle of 180˚, -1 angle of -45˚, -2 downward angle of 180˚). B. Posture, relative number of times different eating and reaching postures were used. C. Number of supporting limbs used by animals when eating and reaching. D. The number of times that different head configurations were used to bring food to the mouth, with a score of "0" indicating that a food item was reached for with the mouth and a score of "4" indicating that the hand brought a food item to the mouth where it was taken with a discrete bite.

The most frequently occurring stance was sitting on the haunches (see Laird et al., 2022 for a description of the relationship between substrate and food type in capuchins). Less frequently animals could be standing on four limbs, three limbs, two limbs and even one limb (Figure 2C). A sitting posture is described as an euarchontoglire trait that has been documented in animals feeding on a horizontal surface (Reghem et al., 2011; Whishaw et al., 1988).

When a food item was brought to the mouth by a hand, the head moved upward, placing the mouth in a horizontal orientation, and so the mouth/head was not advance to take the food from the hand. Other head orienting movements seldom occurred (Figure 2D). Thus, the main movement of getting the food to the mouth involved the hand. Occurrences in which the head was directed to an item, the most frequent of which had an animal holding a stick with both hands and reaching with its mouth to chew, or when an animal was attempting to break a food item loose from its stem when grasping it by the mouth, were infrequent and were not analyzed.

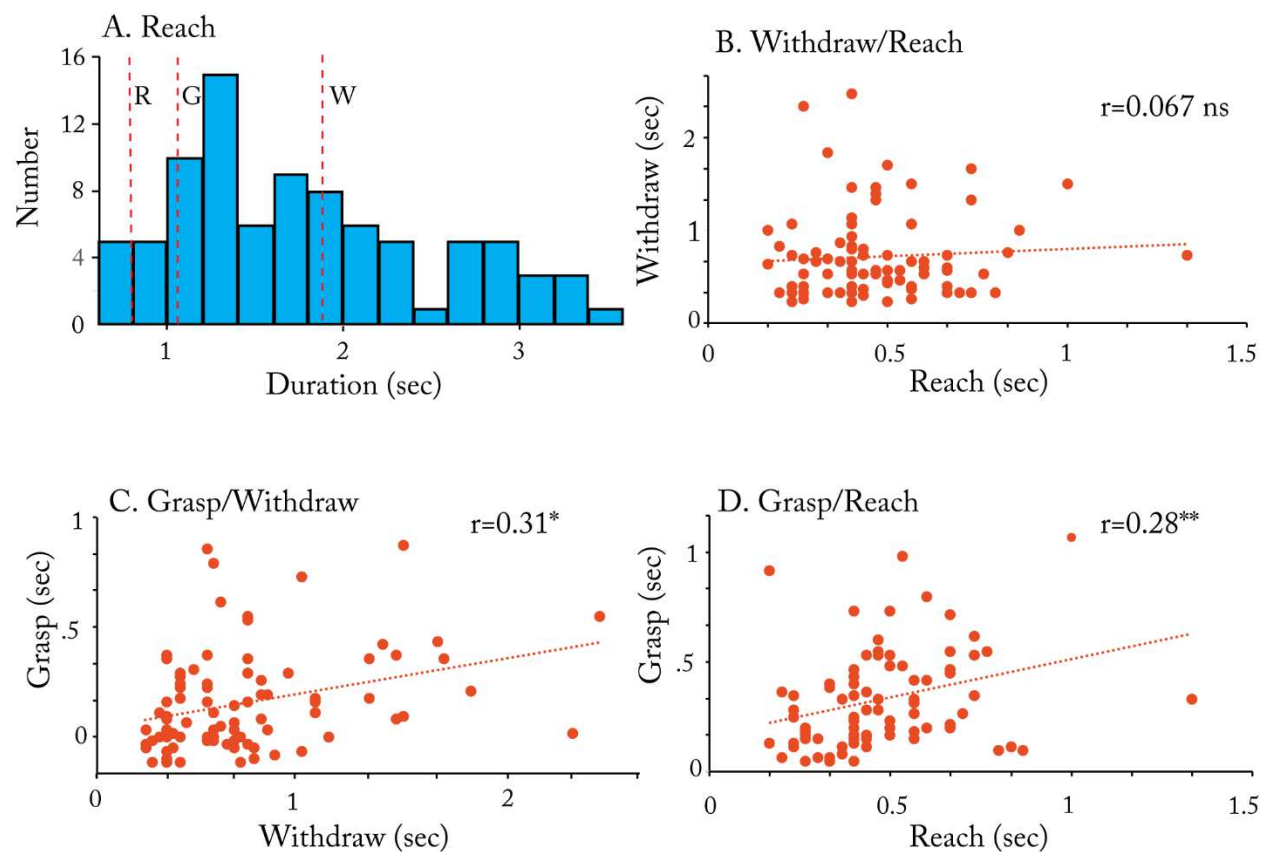## Variability in Reaching and Reach Component Duration

We found variability in the duration of reaches and the durations of each component movement, suggesting flexibility in use of reach, grasp, withdraw components. A total of 88 reaching acts were measured from adult animals picking *Ficus ovalis,* a grape sized fig. All acts were those associated with an

immediate withdraw-to-eat, in which the food item is brought directly to the mouth after grasping. Reaching durations lasted from less than 1 s to more than 3 s, and variability was featured in each of the component movements (Figure 3). Figure 3A illustrates the distribution of the time taken to perform the reaching act and the vertical dotted lines give the average durations of the subcomponent movements of reaching: the reach, the grasp, and the withdraw-to-eat. Factors influencing movement durations likely included: the distance that an animal was reaching, the involvement of the non-reaching hand in manipulating a branch containing a target item into a location from which it could be grasped by the reaching hand, the movements of the hand over and around vegetation in order to obtain purchase a target item, and even the slowing of a movement to perform adjunct movement such as the spitting out of food to make way for a new food item to be placed in the mouth (see below).

Figure 3

Reach, Grasp and Withdraw-to-Eat Component Time

Note. A. Distribution of all total reach times, with vertical dotted lines indicating the mean duration of the reaching components: reach (R), grasp (G) and withdraw-to-eat (W). B. Relationship between mean withdraw-to-eat movement duration and mean reach duration. C. Relationship between mean grasp duration and mean withdraw-to-eat movement duration. D. Relationship between mean grasp duration and mean reach duration. Large variation in reaching times and component times associated with low correlation value suggest independence of the component movements of reaching.

We found that there were only weak correlations between the reach, grasp, and withdraw-to-eat durations. The correlations suggest that, although the reach, grasp and withdraw-to-eat always occur in the same order, the duration of each movement is variable and is associated with factors other than those related to the duration of the other movement components. The correlation between the durations of the reach and the withdraw-to-eat was not significant, $r(86) = .067$, $p > .05$. Although there were significant correlations between the grasp and the reach durations, $r(86) = .31$, $p < .05$, and the grasp and the withdraw-to-eat, $r(86)$

= .28, p < .05, inspection of the figures confirm that these correlations are not high (Figures 3B-D). Taken together, the variability in movement component durations show that there is substantial autonomy in each of the component movements of capuchin reaching.
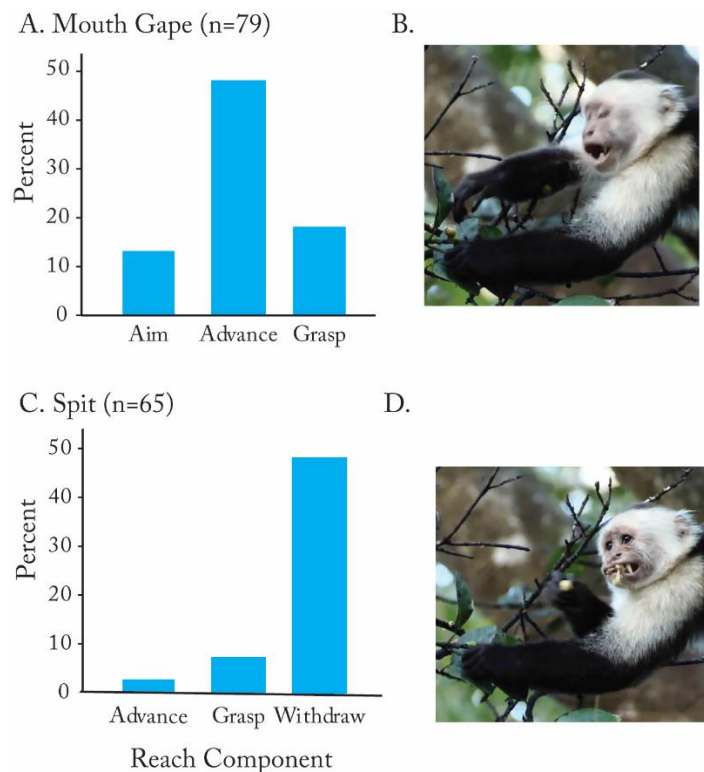
Adjunct Oral Movement Accompany Reach Component Movement

Associated with both reaching for a food item and withdrawing a food item to the mouth, the capuchins were observed to make adjunct oral movements (for a review of many reports of adjunct oral movements accompanying hand movements, see Vainio, 2019). These movements were documented as capuchins foraged for *Ficus ovalis* (Video S1 and Figure 4). In 79% of 98 reaches, the capuchins made a mouth gape. The majority of mouth gapes occurred as the hand was advanced to the fruit (48%). Less frequently, mouth gapes occurred as the hand was in the aim position, raised and ready to be advanced to the target, (14%), or, somewhat later in the reach, as the hand was positioning to grasp (18%). Mouth gapes did not occur on the withdraw-to-eat (Figure 4A, B).

Spitting food out of the mouth occurred on 57% of 98 withdraw-to-eat movements (Figure 4C, D), and spitting occurred usually as the hand approached the mouth (Video S1). During spitting, the hand often visibly slowed its approach to the mouth, apparently so that the animal could clear its mouth to accept a new fruit item. Food spitting behavior was mainly associated with eating *Ficus ovalis*, suggesting there were some portions of the fig being rejected.

Figure 4

Adjunct Oral Movement Associated with Reaching for Ficus ovalis

Note. A. Percent of observations during which mouth gapes occurred during different component movements of the reach as the hand advances to the food. B. A capuchin named *BD* makes a mouth gape that occurred as the hand was advanced to grab a fruit item. C. Percent of observations during which spitting movements of the mouth occurred with different components of an immediate withdraw of a fruit item to the mouth. D. *BD* makes a spitting movement that occurred as the hand was withdrawn to the mouth. Adjunct oral movements suggest independence of hand and mouth control for reaching and eating.

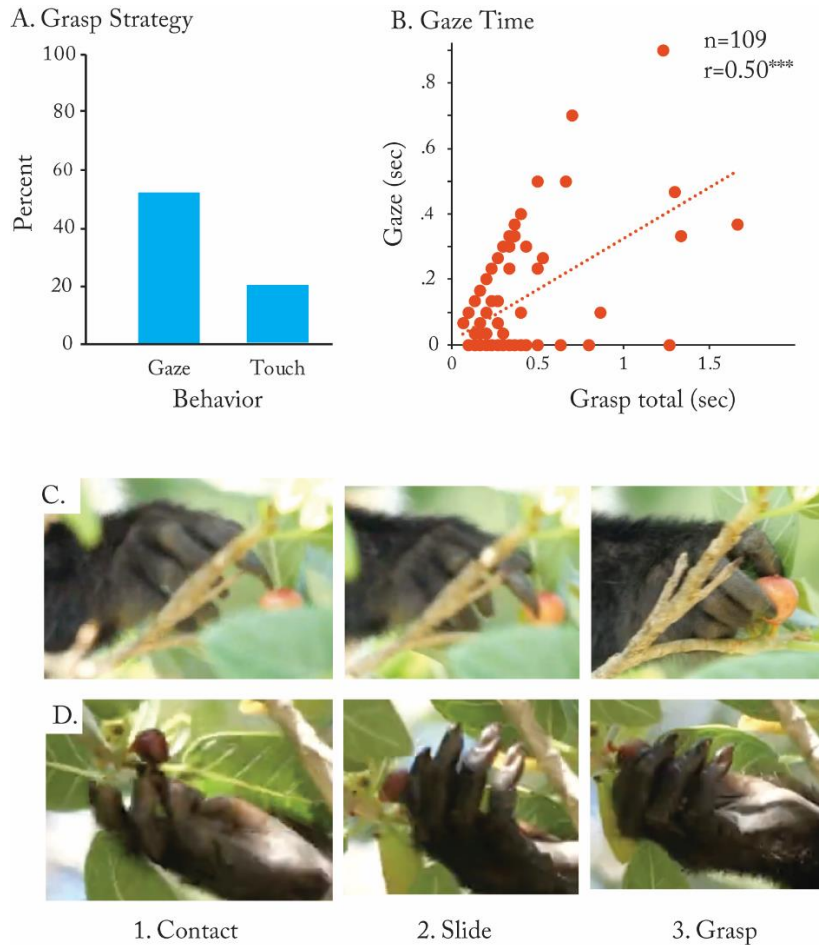**Gaze and Touch Strategies are Used for the Grasp**

Figure 5A illustrates the relation between gaze duration and total time taken to grasp a fruit item. There was a significant relationship between gaze duration and grasp time, $r(107) = .50$, $p < .001$, but both gaze and grasp duration were variable, lasting from less than half a second to as long as one second. Nevertheless, about 50% of grasps were not associated with gaze being directed at the food object during grasping and about 15% of grasps were associated with touches that contributed to orienting the hand to grasp (see Figure 5B; Video S2). Thus, for about half of all grasps, gaze was not directed to the food item as it was grasped. This may be why many grasps were associated with hand orienting movements seemingly mediated by touch (for a description of the use of touch for assessing fruit ripeness in foraging capuchins, see Melin et al., 2022). Figure 5C shows a photo from a video sequence in which a capuchin contacts a fig with the second finger and maintains contact as it slides its finger over the object before grasping. Figure 5D shows a photo from a video sequence in which a capuchin moves its palm across a fig as if locating the fig, and then reverses its trajectory to grasp the fig.

Gaze and Somatosensation Associated with Immediate Withdraw-to-Eat

The number of hands used for reach and withdraw-to-eat movements indicated that whereas one or two hands could be used for reaching, withdraw-to-eat movements were made with one hand. When reaching for food, the capuchins used one hand to reach for a food item for approximately half of their reaches (n = 304), and for the other half of their reaches used the assistance of a second hand (n = 293; Figure 6A). When only one hand was used, the other hand was used for support, either on the substrate or holding onto a branch (Figure 6B). When two hand were used, one hand grasped a branch containing fruit and manipulated it into a position from which the other hand could grasp the fruit (Figure 6C). Regardless of the grasping strategies used to obtain fruit items, the fruit was always brought to the mouth with one hand. One-handed withdraw-to-eat might be expected as the fruit items were relatively small.

The frequency with which fruit items were placed between/grasped by the incisors upon immediate withdraw-to-eat is summarized in Figure 6D. For 60 of 128 immediate withdraw-to-eat movements, the item was grasped with a precision grasp and transferred to the incisors with the palm in a relatively vertical, 90^0 supinated position (Figure 6E). For 69 of 128 withdraw-to-eat movements, the food was held in a whole hand grasp and was transferred to the incisors with the hand fully supinated (Figure 6F). Transfers of food items from the hand to the mouth involved one relatively discrete movement, with few transfers involving repeated bites of the food item, and no transfers missing placement to the incisors and requiring a correction. Nevertheless, most observations of food transfer involved the transfer of fruit items that were easy to take with a bite. There were instances in which the capuchins were observed to grasp items with the premolars, but these were either instances in which they were trying to dislodge a fruit item such as *Bromelia pinguin* (a food item growing in clusters) with their mouth or were biting the bark from a stick with the mouth. These activities were not formally investigated.
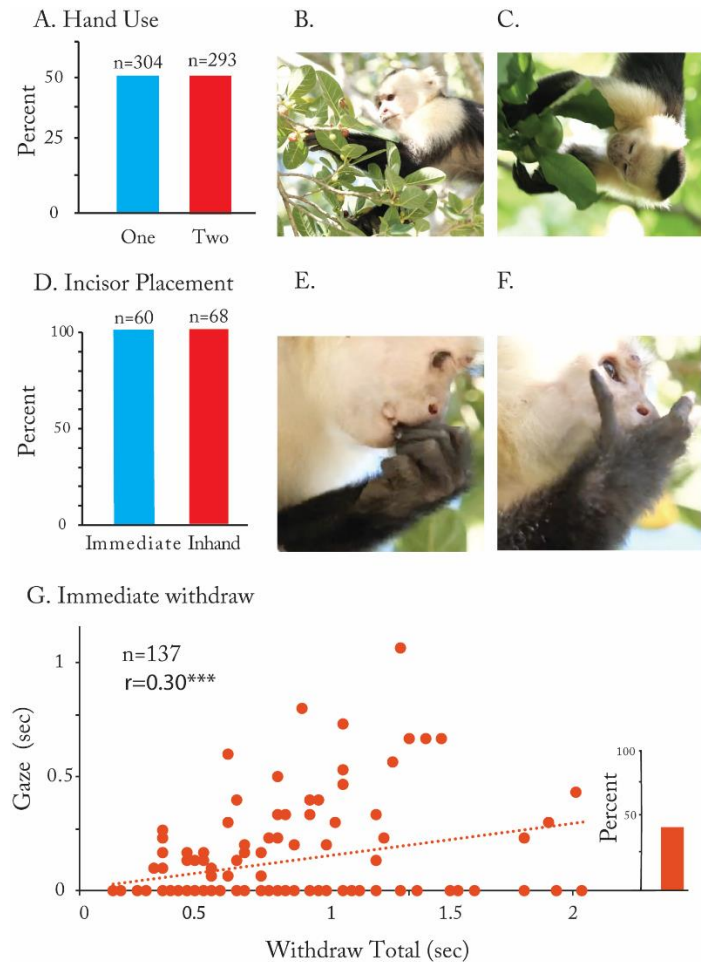
Precision grasps were used to grasp food items that were small (e.g., *Ficus ovalis* and *Ficus cotinifolia*, which are grape sized) and whole hand grasps to obtain food items that are larger (e.g., *Spondias mombin* and *Diospyros salicifolia*, which are plum sized; Figure 6D-E). Of 89 grasps, 42% (37/89) were made using a precision grip and 58% (49/89) were whole hand grips. A correlation between grasping posture and food size gave a significant correlation between grip type and food size, $r(87) = .74$, $p < .001$. Of the 89 observations, there were 10 where precision grips were used for larger food items and one where a whole hand grip was used for a small food item.

Figure 5

Grasp and Gaze

A. Grasp Strategy

B. Gaze Time

n=109
r=0.50***

C.

D.

1. Contact   2. Slide   3. Grasp

Note. A. Grasp strategy shows that about half of all reaches were not associated with concurrent gaze and that about a quarter of all reaches featured hand touches to the target before grasping. B. There is a significant relationship between total gaze time and total grasp time, but the correlation is not high as about half of reaches are not associated with concurrent gaze. C. Example of a precision grasp made with a pronated hand in which the fruit *Ficus ovalis* was touched by a finger that appeared to guide the grasp. D. An example of a grasp in which a supinated hand appears to identify a *Ficus ovalis* fruit item location using touch, which then appears to guide the grasp.

Of 139 observations for which the face was oriented so gaze could be ascertained, there was a weak association between gaze duration and time to withdraw-to-eat, r(137) = .30, $p < .05$ (Figure 6G). Less than 50% of immediate withdraw-to-eat movements were associated with gaze directed to the food item during the withdraw-to-eat (Figure 6D). A similar absence of an association between gaze and immediate withdraw-to-eat for relatively small food items is reported for macaques and for humans (de Bruin et al., 2008; Hirsche et al., 2022; Sacrey et al., 2011).

An examination of in-hand withdraw-to-eat movements showed that for 94% (169/179) of the withdraw-to-eat movements, the food was manipulated into a precision grip (Figure 3E). Because 97% of in-hand holding movements were with larger fruit items, at least one objective of in-hand manipulations involved moving the object from a whole hand grasp to a precision grasp. Of 104 in-hand withdraw-to-eat movements in which food was transferred to the mouth and a bite was taken from the food, 87 (83.6%) were associated with hand adjustments including releasing and regrasping the food item so that it was placed/replaced in a precision grip.

Figure 6

Hand Use During Reach and Withdraw-to-Eat Movement

Note. A. One or both hands could participate in fruit picking as only one hand picked, whereas the other provided support or one manipulated a branch as the other reached. B. A capuchin named *B* uses one hand to reach. C. Capuchin *B* uses one hand to manipulate a branch and the other hand to reach. D. *B* presents fruit to be grasped with the incisors from a precision grasp or a whole hand grasp. E. A capuchin named *PA* presents a fruit item to the mouth with a precision grasp. F *PA* presents a fruit item to the mouth with a whole hand grasp. With the precision grasp the hand was partially supinated (palm-vertical) and with a whole hand grasp the hand is fully supinated (the palm the facing mouth). G. Relation between gaze directed to the fruit during immediate withdraw-to-eat and total withdraw-to-eat movement time showing that the relation was weakly significant (r = .30, *p* < .05) because almost half of immediate withdraw-to-eat movements were not associated with gaze (insert).

Gaze, Precision Grip and Hand Posture Associated with Withdraw-to-Eat

From 417 in-hand withdraw-to-eat movements, holding was most frequently associated with two hands (Figure 7A, C), whereas withdrawing the food item to the mouth was associated with one hand (Figure 7B, D). The shift from two hands to one hand yielded a significant Pearson Chi-Square value, Chi-Square(1) = 175, *p* < .001. The significant effect suggests a preference for two-hand holding *versus* one-hand withdraw-to-eat for the fruit item sizes that were being eaten.

During food holding, a food item could be passed between the hands, picked at with one hand while being held with the other, or manipulated to an orientation for placement in the mouth. An analysis of the grasp for withdraw-to-eat showed that for 391 of 417 (94.4%) of the movements, the food item was held in

Figure 7

In-hand Withdraw-to-Eat and Gaze

Note. A. A capuchin named *CZ* manipulates a fruit item to place it into a precision grasp under gaze. B. *CZ* presents the food item held with a precision grasp and with a partially supinated hand (palm-vertical) to the mouth. C. The high incidence of two-handed fruit handling. D. The high incidence of one handed withdraw-to-eat. E. The relation between gaze time and total handling and withdraw-to-eat time was significant, r(273) = .98), showing that gaze related activity accounted for most of the food handling/withdraw time and withdraw time variation. The insert (Percent) shows that all food handling events were associated with gaze directed to the food manipulation movements.

a *Cebus* precision grip (using digits one, two, and also the palm) and the palm was in a 90º orientation, with a palm-in orientation, for food transfer to the mouth. Because most of the food items taken from an in-hand holding position were the larger fruit items, this result suggests that the objective in handling the food item was to regrip an item so that the item was held with a *Cebus* precision grip for presentation to the mouth. It was observed that as the capuchins took a bite from a food item, they also frequently adjusted their hand position, by quickly releasing and regrasping the item, to maintain a *Cebus* precision grip and hand posture (see above). On those instances on which both hands withdrew a food item to the mouth, a *Cebus* precision grip was used and both hands were similarly oriented in a palm-vertical posture.
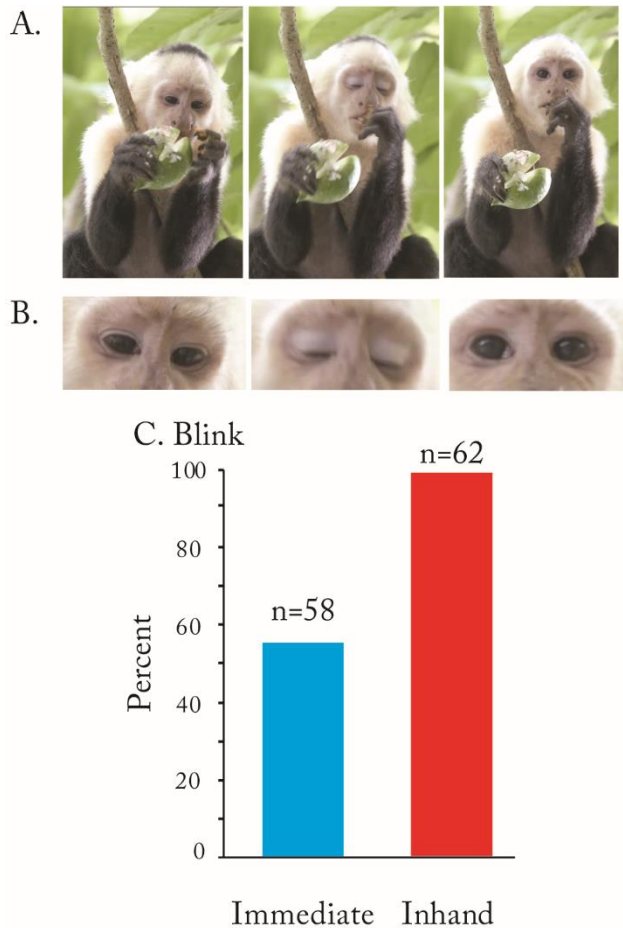
Measures of the duration of gaze anchoring on the food item, including holding/manipulating and withdraw-to-eat movement relative to the total duration of holding and withdrawing, were obtained from 279 holding and withdraw-to-eat events (Figure 7E). The number of withdraw-to-eat movements associated with gaze anchoring measures was limited to those in which the face and eyes could be seen. Because gaze was only disengaged for a brief and relatively constant duration of time during the latter portion of the withdraw-to-eat, nearly all variation in time is associated with the period of gaze anchoring (Figure 7E). This relationship was supported by a significant correlation, $r(275) = .98$, $p < .001$, between gaze duration and total handling and withdraw-to-eat time. Gaze was also maintained during the initial portion of the withdraw-to-eat itself, and there was a significant relationship between gaze duration during withdraw-to-eat and total withdraw-to-eat time, $r(275) = .709$, $p < .001$. The average point of occurrence of eye disengage during the withdraw-to-eat movement was at a point 70.1% of the way through the withdraw-to-eat (between the first frame of the video where the wrist began to approach the mouth to the point that wrist movement stopped as the food was transferred to the incisors).

A Blink Indicated the Point of Eye Disengage

A blink, as described in humans and macaques (de Bruin et al., 2008; Hirsche, 2022), was reliably associated with gaze/head disengage during in-hand withdraw-to-eat movements (Figure 8, Video S3). A blink by a capuchin that occurred just as gaze was disengaged during an in-hand withdraw-to-eat movement, after a capuchin had fished some pulp from *Stemmadenia obovata* with its index finger is show in Figure 8A. The blink was associated with raising the head from a downward orientation, in which gaze was directed to the food, to a horizontal position, in which the food was accepted by the mouth (Figure 8B).

The relationship between immediate withdraw-to-eat movements and blinks was not as clear as it was for in-hand withdraw movements and blinks (Figure 8C). Of 55 immediate withdraw-to-eat movements in which the face was visible, only half were associated with a disengage blink, whereas of 98 in-hand withdraw movements, 96 were all associated with a disengage blink. As noted in the sections related to Figure 7, for immediate withdraw-to-eat movements, gaze/disengage often occurred before an item was grasped and so might be missed if the head was not oriented to the camera. For in-hand withdraw movements, the blinks were more seemingly time influenced and were initiated approximately at three quarter of the way through the withdraw-to-eat movement (the initiation of a blink preceded head disengage), as the hand transitioned from holding and manipulating a food item to placing the food item in the mouth.

Figure 8

Blink and Withdraw-to-Eat

Note. A. A capuchin named *AP* uses a finger to fish pulp from *Stemmadenia obovata* and withdraw the pulp to the mouth with an index finger. In the sequence, the finger is inserted into the middle of the fruit to obtain a piece of pulp and then the finger takes the pulp to the mouth. B. Finger fishing is associated with gaze anchoring and gaze is disengaged with an associated eye blink during the withdraw to the mouth. C. The percent of blinks with immediate withdraw-to-eat movements were not high as blinks could occur before a fruit item was grasped, *versus* the high incidence of blinks occurred with in-hand withdraw-to-eat movement because gaze was always directed to the fruit when it was handled.

Discussion

This study examined food handling and eating during natural foraging by the platyrrhine primate, *Cebus imitator*. The question asked is whether *Cebus* uses a visually mediated strategy to orient food items held in the hand for withdraw to the mouth for eating, as do catarrhine primates, or whether it uses a somatosensory strategy of reaching with the mouth to take food from the hand, as do strepsirrhine primates. The use of a sitting posture, flexible use of reach, grasp and the withdraw-to-eat movements, and unilateral and bilateral fruit picking and handling highlight *Cebus* motoric skills in fruit picking. A withdraw to bring food to the mouth after grasping features the use of somatosensation along with vision. An in-hand withdraw-to-eat, in which food is positioned in a *Cebus* precision grip for optimal presentation to the mouth, is always assisted by vision. The application of vision to food handling during in-hand manipulation and withdraw-to-eat may represent a platyrrhine contribution to the evolution of the visually mediated cognitive and manual skill observed in catarrhines.

Although capuchins might glance at an item before reaching, disengage often occurred before food was grasped and the grasp itself was often associated with target touching (see Melin et al., 2022 for a description of touch use in estimating fruit ripeness by capuchin monkeys). The use of a touch strategy to grasp might additionally be related to reaching through leaves that obscure visualization of the object, but we noted that animals might also look away from objects that were unobscured before grasping them. Nevertheless, small items were usually grasped with a *Cebus* precision grip involving the first two digits and palm and large items with a whole hand grip. Items of both sizes could be brought to the mouth with an immediate withdraw-to-eat movement without visual monitoring. That small food items can be grasped and brought to the mouth without visual monitoring has been reported for humans fitted with eye-tracking glasses. The same studies show that visual occlusion does not disrupt the accuracy of this form of withdraw-to-eat, supporting the idea that the basis of hand control of small objects is mediated largely by touch (de Bruin et al., 2008; Karl et al., 2012; Sacrey et al., 2011). In short, touch is important for grasping food and for the immediate presentation of food to the mouth in *Cebus*.

In-hand food manipulation and withdraw-to-eat were always associated with vision and this visual control appeared to be directed toward obtaining an optimal finger grip for food presentation to the mouth. Studies on capuchin grips describe a precision grip in which the thumb holds an item against the side of the second digit (Christel & Fragazy, 2000; Costello & Fragazy, 1988; Spinozzi et al., 2004; Truppa et al., 2019, 2021). Here we noted that the first and/or second digit could also press a food item against the palm. These various grips were difficult to distinguish, but when used collectively as a *Cebus* precision grip, they resulted in a food item being held so that it protruded from the radial side of the hand. When the hand is presented to the mouth in a palm vertical orientation, the food item is positioned to be grasped with the incisors. Thus, although capuchins may not display the variety of hand shaping movements of catarrhine primates, their manipulatory movements have the objective or orienting a food item in the hand for mouth presentation. Preplanning of food manipulation using precision grasping in humans has been suggested to be directed to end-state comfort; i.e., the ultimate disposition of the object (Rosenbaum et al., 2012). End-state comfort also appears to be the objective of capuchin visually mediated in-hand manipulation and withdraw-to-eat, as prepositioning a food item in-hand promotes the ease of hand-to-mouth transfer.

Initial speculation about the visual control of hand shaping suggested that it evolved, in part, for insect or fruit harvesting in stem primates occupying a fine branch niche (Cartmill, 1972, 1974, 1992, 2012; Scott, 2019; Sussman & Raven, 1978; Sussman et al., 2013). Because strepsirrhine primates do not use visually mediated in-hand food manipulation or precision grips for object grasping, whereas platyrrhine primates (as shown here) and catarrhine primates (Hirsche et al., 2022) do, it is likely that a visually mediated withdraw-to-eat movement evolved in a stem anthropoid primate. This conclusion is consistent with the idea that each of the component movements of reaching may have its own evolutionary history (Grant & Conway, 2019; Jeannerod,1981; Jeannerod et al., 1995, 1998; Sartori et al., 2015; Whishaw et al., 2016). The visual monitoring of food in-hand may be an evolutionary stage that preceded and/or contributed to the visual control of how food is grasped (Hirsch et al., 2022).

For *Cebus,* the long durations of visual monitoring of food in-hand of vs the short durations of visual monitoring of food with grasping is striking. In-hand visual monitoring and manipulation is directed toward the intrinsic (what) food feature such as ripeness as well as extrinsic (where) food features such as shape and size. A memory for these features of food is relevant to its disposition, for example, whether food should be directed to the incisors or premolars. This working memory for object and spatial features of food may be origin of the what/where working memory reported to be mediated by agranular prefrontal cortex (Kaas, 2019; Preuss & Goldman-Rakic 1991; Williams et al., 2010; Wilson et al., 1993). Anatomical findings show that *Cebus* has a large agranular prefrontal cortex (Cruz-Rizzolo et al., 2011). Additionally, *Cebus* has a deep penetration of the direct projection of the corticospinal tract to cervical motor neurons (Bortoff & Strick, 1993), as also occurs in catarrhines. This anatomical feature may enable the sensorimotor control of inhand food items. In short, it is possible that these anatomical features are extensions of the visual system that aid in the cognitive/motoric skills required for in-hand food handling (Karl & Whishaw, 2013). Additionally, visually-related withdraw movements may feature a visual contribution to the

oromanual area of frontal cortex described in rodents (An et al, 2022). Once developed, such visual working memory skills could be exploited in a range of conditions by any appendage.

The association of eye-disengage with an eye blink as food is brought to the mouth observed in *Cebus* is also found in humans and macaques (de Bruin et al., 2008; Hirsch et al., 2022; Karl et al., 2012; Sacrey et al., 2011). Proposed explanations for blinks include the ideas that they are associated with visual focus and/or related shifts in brain networks. With respect to focus, the idea is that visualizing a target held in the hands requires accommodation (Kiorpes, 2019). A blink may represent a release from the strain of accommodation (Ang & Maus, 2020) and may then facilitate focusing when looking elsewhere (Jaschinski et al., 1996). Blinks, however, may also signal a brain network change (Brych & Händel, 2020; Nakano et al., 2013). Although *Cebus* visually tracks a food item during the first portion of a withdraw, as the blink and head raising co-occur, vision is disengaged and subsequent food placement in the mouth is guided by touch. A blink may signal a change from using a visual network involved in food tracking in the initial portion of withdraw to a somatosensory network that completes the withdraw movement as food is placed in the mouth. Because strepsirrhines do not use a visual assisted withdraw-to-eat or an associated blink, blink-related disengage, this behavior likely also evolved in stem anthropoids in association with the development of cognitive systems that applied vision to getting food from the hands to the mouth.

A caveat to the idea that visual object monitoring is used to adjust food items to an optimal hand grasp relates to the similarity of many of the food items for which *Cebus imitator* were foraging. The figs and plum-sized fruits varied in size but were round. They thus might not be representative of food items that protrude from the hands and so require more handling for mouth presentation (Truppa et al., 2021). Incidental observations of the handling of other items did show that the capuchins could use other hand/mouth transfer strategies. When holding sticks upon which they chewed, the capuchins usually brought their mouth to the stick rather than bringing the stick to the mouth. They also brought their mouth to *Luehea candida*, a large shell containing seeds, when attempting to obtain seeds from them. When shaking *Luehea candida* shells to remove their seeds, capuchins were also observed to catch and bring freed seeds to the mouth in an open palm. Finally, as reported in the results, when removing aril from *Stemmadenia obovata*, they used only an index finger. Nevertheless, for these behaviors including shaking objects and using a single digit, *Cebus* usually used a palm-vertical strategy similar to that used when withdrawing fruit to the mouth.

In conclusion, the present study gives an affirmative answer the question of whether platyrrhine *Cebus imitator* uses vision for in-hand food manipulation and withdraw-to-eat. Parsimony argues that visually mediated in-hand manipulation and withdraw-to-eat behavior of *Cebus* has its origins in a stem anthropoid that displayed the behavior. In-hand food manipulation and withdraw-to-eat could be further investigated in relation to the many other kinds of food consumed by capuchins (Truppa et al., 2021). The presence of food handling during withdraw-to-eat along with blinking behavior could also investigated in other platyrrhine families and species. Future study of platyrrhines could investigate the suggestion made here that the visual control of withdraw-to-eat influences the evolution of the visuocognitive control of grasping and object manipulation more generally.

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Supplementary Materials

Video S1. A reach in which a capuchin named *B* is eating *Ficus ovalis*. The capuchin visually disengages a fruit item with a blink and head movement that brings the mouth to a horizontal orientation before completing the reach and making a precision grasp followed by a withdraw-to-eat movement. Note the adjunct mouth gape as the hand advances to the fruit target and the adjunct spitting movements during the withdraw-to-eat movement. Note also that the right hand manipulates the branch so that the fruit can be obtained with the left hand. https://doi.org/10.6084/m9.figshare.25029833.v1

Video S2. A capuchin named *MT* makes an underhand touch-associated precision grasp. The target fruit *Ficus ovalis* is first touched and then the hand reverses movement direction in order to make a precision grasp of the item. https://doi.org/10.6084/m9.figshare.25029857.v1

Video S3. A capuchin named *AP* pulp fishes with a finger in *Stemmadenia obovata* fruit. *AP* makes a withdraw-to-eat movement associated with visual disengage, a blink and a lift of the mouth to a horizontal orientation of accept the food item from the finger with the incisors. https://doi.org/10.6084/m9.figshare.25030097.v1