



# Evolutionary History of food Withdraw Movements in Primates: Food Withdraw is Mediated by Nonvisual Strategies in 22 Species of Strepsirrhines

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## Abstract

Anthropoid vision contributes not only to reaching and grasping but also to the orienting of a food item during the withdraw movement to precisely place it in the mouth for eating. The evolutionary history of this visual control of feeding is not known. It likely evolved from the nonvisual control of the hand that is used with good effect for eating in many non-primate animal species. Strepsirrhines are a relatively large monophyletic group, diverging near the base of the primate cladogram, and described as using vision to reach for food. It is not known whether they use vision to orient food items during the withdraw movement. Video recordings of 7,464 withdraw movements from 22 species of captive strepsirrhines eating their normal food provisions were used to assess whether and how vision contributes to the withdraw movement. The constituent acts of withdraw movements, head orientation, body posture, ground-withdraw and inhand-withdraw, were assessed using frame-by-frame video inspection. Strepsirrhines were versatile in using their hands to get food to the mouth. They displayed variation between and within families that were weakly related to phylogenetic relationships and mainly related to feeding niches. There was no evidence that any species used vision to assist with the withdraw movement. Instead strepsirrhines used mouth reaching to take food from the hand and/or perioral contact to positioning food for biting. Our findings support two hypotheses: that visual mediation of food orienting for placement in the mouth during the withdraw movement is an anthropoid innovation, and that the evolution of the visual control of feeding was not a singular event.

**Keywords** Evolution · Strepsirrhines · Grasping abilities · Visual control

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## Introduction

Primates are proposed to be special in their capacity to use vision to guide reaching and grasping (Leopold et al., 2020). Both Cartmill's (1972, 1974, 1992, 2012) visual-predation theory and Sussman's (Sussman & Raven, 1978; Sussman, 1991; Sussman et al., 2013) primate-angiosperm theories posit that a stem primate evolved visual control of the hands for the capture of small food items on the terminal branches of trees. Nevertheless, these theories are unclear with respect to the details of this evolution because nonvisual control of the hand is used with good effect for eating in many non-primate animal species (Iwaniuk & Whishaw, 2000; Sustaita et al., 2013; Whishaw & Karl, 2019) and also because the visual control of the hand may not have evolved as a single process. With respect to the latter point, Jeannerod's (Arbib, 1981; Jeannerod, 1981; Jeannerod et al., 1995, 1998; Sartori et al., 2015; Grant & Conway, 2019) dual visuomotor channel theory proposes that visual control of the hand involves at least two neural processes, one for the reach and one for the grasp. The reach directs the hand toward the extrinsic (spatial) features of a target, and the grasp directs hand shaping in relation to the intrinsic (size, shape) features of a target. These studies suggest that hand use for eating is a composite movement in which each component has its own objective, sensory control and likely its own evolutionary history (Whishaw & Karl, 2019).

A distinct third hand movement, the withdraw movement, brings an item grasped by hand to the mouth (Karl & Whishaw, 2013; Whishaw & Karl, 2014, 2019; Karl et al., 2018). A study of a free-ranging population of long-tailed macaques (*Macaca fascicularis*) shows that their withdraw movement is achieved with visual assistance (Hirsche et al., 2022). The macaques look at a food item that they pick up, or that they hold in a hand, to orient the item so that it can be appropriately placed in the mouth. Visually-mediated food orienting is especially useful for food that protrudes from the hand because it contributes to feeding efficiency by enabling the food item to be taken by the mouth with a precise bite. The visually-guided withdraw movement of macaques is similar to that used by other anthropoid species (both Old World Catarrhines e.g. chimpanzees *Pan troglodytes* and capuchin monkeys *Cebus albifrons* and New World Platyrrhines e.g. squirrel monkeys *Saimiri oerstedii*), including humans, suggesting that it is a behavior common to anthropoids (de Bruin et al., 2008; Sacrey et al., 2011; Karl & Whishaw, 2013; Hirsche et al., 2022). The presence of visual control of the withdraw movement of anthropoids raises the question of whether strepsirrhines similarly use vision to assist their withdraw movement. Strepsirrhines are of interest because they are a relatively large monophyletic group of Euarchontoglires near the base of the primate

cladogram. They use vision to reach for food (Reghem et al., 2011; Perrenoud et al., 2020) but lack the hand-shaping movements featured in the visual control of precision grasps described for anthropoids (Bishop, 1964; Christel, 1993; Christel & Frigaszy, 2000; Pouydebat et al., 2008; Macfarlane & Graziano, 2009; Marzke et al., 2015; Peckre et al., 2016; Scott, 2019).

To gain insight into whether strepsirrhines use visually-guided withdraw movements, the present study examined the withdraw movements of 22 species of captive strepsirrhines representing six of the seven strepsirrhine families. Two types of withdraw movements, ground withdraw movements, in which a food item is brought by hand from the ground to the mouth, and inhand withdraw movements, in which a food item held in the hand is transferred to the mouth, were identified in video recordings of feeding of strepsirrhines. Ratings of body, head, and hand movements were made from frame-by-frame inspection of the video records to identify the sensory control of the withdraw movements.

## Methods

### Subjects

Data were collected from video recordings of 84 individuals (42 female, 42 male) of 22 different species of strepsirrhine primates. The sample included six of the seven strepsirrhine families: Daubentoniidae, Cheirogaleidae, Indriidae, Lemnidae, Lorisidae and Galagidae. The video recordings were previously compiled in Peckre, Fabre et al. (2019). Greater bamboo lemurs, *Hapalemur simus*, were video recorded at Vincennes Zoo (Paris, France) by L.P. Grey slender lorises, *Loris lydekkerianus*, and Senegal bushbabies, *Galago senegalensis*, were recorded at the Antwerp Zoo (Antwerp, Belgium) by A.-C.F. The other species were video recorded at the Duke Lemur Centre (Durham, NC, USA) by A.-C.F. Each animal was video recorded in its home enclosure for several days during its feeding period while eating its usual diet. The usual diet was constituted of different food items, including raw pre-cut pieces of fruits and vegetables in addition to monkey chow (Labdiet Monkey Diet Jumbo Constant Nutrition and ZuPreem Primate Dry Diet). Mealworms were part of the diet for some species. Food items were placed on a flat surface, either on the ground level or on a raised platform. For details of filming, housing conditions, and relative age, see Peckre, Fabre et al. (2019). Animal handling, associated with taking food to the animals, was performed in compliance with the International Primatological Society (IPS) Guidelines for the Use of Nonhuman Primates in Research according to protocol #A089-14-04,

approved by the Duke University Institutional Animal Care and Use Committee.

## Behavioral Scoring

The video recordings of feeding behavior were examined frame-by-frame, and the incidence of the two types of withdraw movement (i.e. ground-withdraw and inhand-withdraw) along with the associated head orientation and body posture were scored in relation to their putative dependence on vision. Four movements were scored: (1) head orientation when picking up food, (2) ground-withdraw by which an item is grasped with a hand and brought directly to the mouth, (3) body posture when taking food from the hand, and (4) inhand-withdraw by which a food item held in the hand is brought to the mouth. The behaviour of a hand bringing the food item to the mouth where it is taken with a single discrete bite is given the highest score for ground- and inhand-withdraw (Hirsche et al., 2022). The scores were designed to distinguish the use of touch and olfaction at the bottom of the scale from visually-guided withdraw, such as that of a macaque, at the top of the scale. Food items picked by mouth and directly swallowed were excluded. As smaller food items were more frequently picked up by mouth and then swallowed (see Peckre, Fabre et al. 2019), most food items included in the analyses were relatively large food items.

*1. Head orientation:* head orientation and distance from food prior to grasping food from the ground. Head orientation was rated on a 5-point scale. It was assumed that if the nose/mouth were proximal to a food item as it was grasped, vision was not being used, whereas if they were distant from an item being picked up, vision might be used.

- 0 – food was grasped with the mouth.
- 1 – the nose was placed near the target as the item was grasped by the hand.
- 2 – the nose was first placed near the target but withdrawn for the hand to advance.
- 3 – the nose was first placed near the target but withdrawn at some distance.
- 4 – the nose was at arm's length from the target as the reach was performed.

*2. Ground-withdraw:* the ground-withdraw movement consisted of using a hand to bring a food item to the proximity of the mouth immediately after it was grasped from the ground. Ground-withdraw was scored on a 6-point scale, with the low end of the scale representing withdraws in which the mouth contributed to grasping and so vision would not be used, whereas the high end of the scale

represented withdraws in which food transport was made entirely by hand and the food was taken with a discrete bite, a movement that might require vision.

- 0 – hand and mouth grasped at about the same time, or the mouth reached for the item as it was grasped by a hand.
- 1 – the hand was rotated (supinated or pronated) after grasping, and the mouth moved to the hand.
- 2 – the hand made a small withdraw as the mouth moved to the hand.
- 3 – the hand and the mouth movement toward each other were approximately equivalent.
- 4 – the hand moved to the mouth with little movement of the head, and the food item was sniffed or touched to the lips before being grasped by the mouth.
- 5 – the hand moved to the mouth with little movement of the head and the mouth opened to directly receive food without sniffing or touching the food to the lips.

*3. Body posture:* orientation of the body and limb position when taking food from the hand with an inhand-withdraw movement. Body posture was rated on a 5-point scale. It was assumed that if an animal was in a quadrupedal stance, its snout would be proximal to a food item when it was grasped, and vision was unlikely to be used, whereas, in an upright posture, vision might be used.

- 0 – a quadrupedal posture with the back horizontal.
- 1 – a three-point posture, with one hand on the floor and the other holding the food, with the back horizontal.
- 2 – a two-point posture, with one or both hands holding a food item, with the back horizontal.
- 3 – a three-point posture, with one hand on the floor and the other holding the food, with the back oblique.
- 4 – a two-point posture with the back oblique and one or both hands holding a food item.

*4. Inhand-withdraw:* an inhand-withdraw movement brought a food item that was held in the hand to the mouth. Inhand-withdraw movements were scored on a 6-point scale. It was assumed that if the hand did not move toward the mouth, vision was not contributing to hand use, whereas if all food transport to the mouth was made by the hand, vision might be used.

- 0 – the hand remained in place, and the mouth moved to the hand.
- 1 – the hand was rotated (supinated or pronated) as the mouth moved to the hand.
- 2 – the hand made a small withdraw as the mouth moved to the hand.

3 – the hand and the mouth movement toward each other were approximately equivalent.

4 – the hand moved to the mouth with little movement of the head, and the food item was sniffed or touched to the lips before being grasped by the mouth.

5 – the hand moved to the mouth with little movement of the head and the mouth opened to directly receive food without sniffing or touching the food to the lips.

## Statistical Analyses

Data were analyzed using a non-probability method in which each species served as a statistical subject (Fuller, 2011). Because there were unequal numbers of animals in groups and because the number of eating movements in each of the animals differed, observations were grouped for the analyses by species, with the result that the number of observations per species ranged from 80 to 651 (mean  $322 \pm 34.5$  per species). Scores were averaged for each variable and each species, and the results were presented as the mean  $\pm$  standard error. Correlations between the different variables were assessed using Spearman-rank correlations (cor.test function; R Core Team 2021).

Strepsirrhines share their phylogenetic history and, therefore, cannot be considered independent data points (Felsenstein, 1985). To address this issue and determine the adequacy of using conventional or phylogenetically informed statistical analyses, we tested the presence of a phylogenetic signal using the multivariate K-statistic (K<sub>mult</sub>) assessed with the R ‘physignal’ function included in the ‘geomorph’ package (Adams, 2014; Adams et al., 2018). The K-value is a scaling parameter for the correlations between species traits relative to the correlation expected under Brownian motion. Values of  $K < 1.0$  correspond to traits being less similar among species than expected based on their phylogenetic relationships. This method requires the use of a phylogenetic tree. We used a consensus tree in v.3 of the 10kTrees Project (Arnold et al., 2010). There was a significant but weak phylogenetic signal in the withdrawal behaviours of strepsirrhines ( $K_{\text{mult}}=0.31$ ;  $p=0.019$ ). We, therefore, computed further phylogenetic Spearman correlations using the phylogenetically independent contrasts assessed using the function ‘pic’ of the ‘ape’ package (Paradis & Schliep, 2019).

## Results

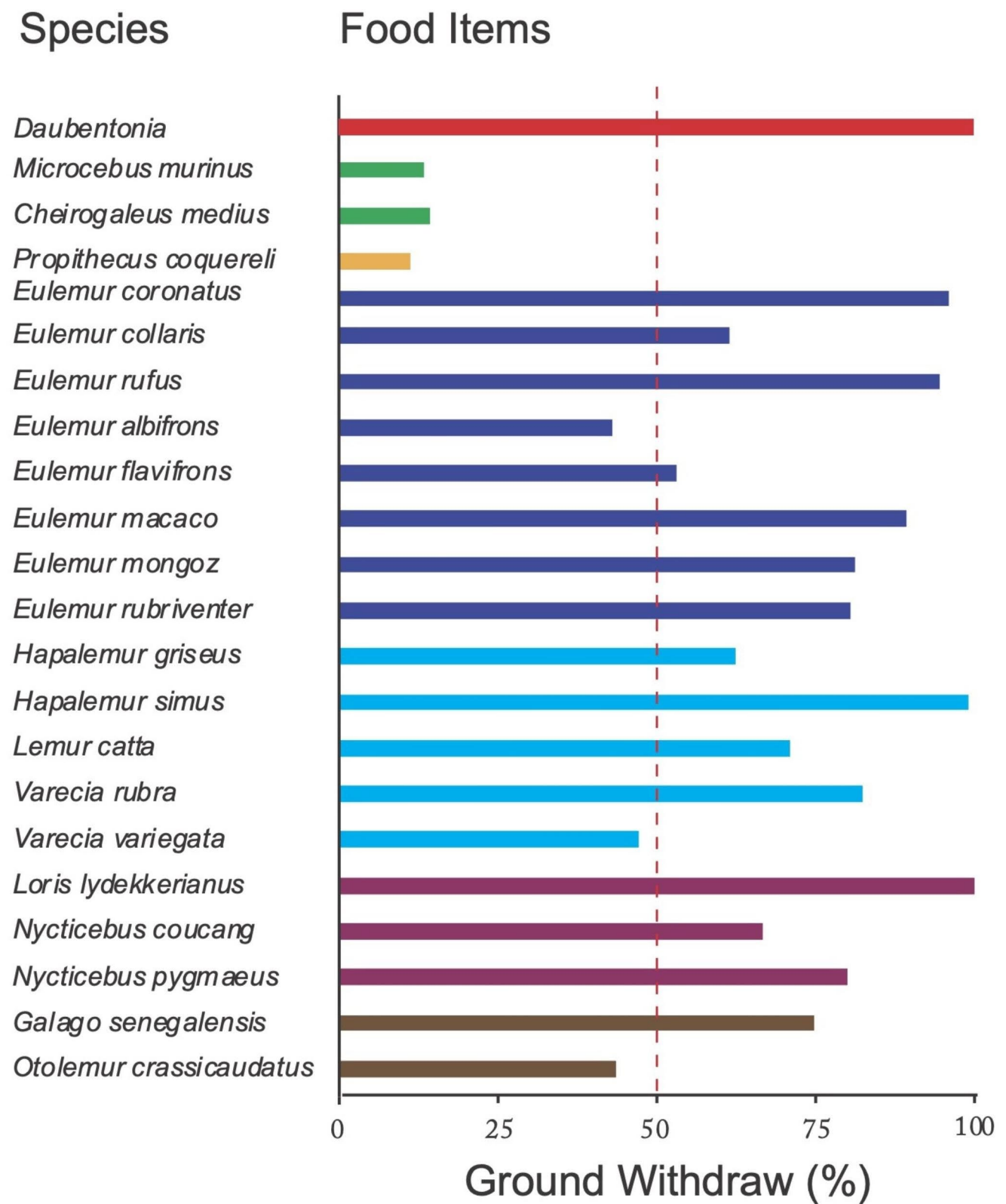
### General Observations

Frame-by-frame counts of the withdraw movements used to bring a food item were based on a total of 1934 food items (mean  $81 \pm 15.2$  per species) that provided 1934 (mean  $80.5 \pm 15.2$ ) ground-withdraw movements and 5530 (mean of  $230.4 \pm 4.9$  per species) inhand-withdraw movements. Because a larger food item could be brought to the mouth repeatedly with inhand-withdraw movements until consumed, there were many more inhand-withdraw movements than there were food items.

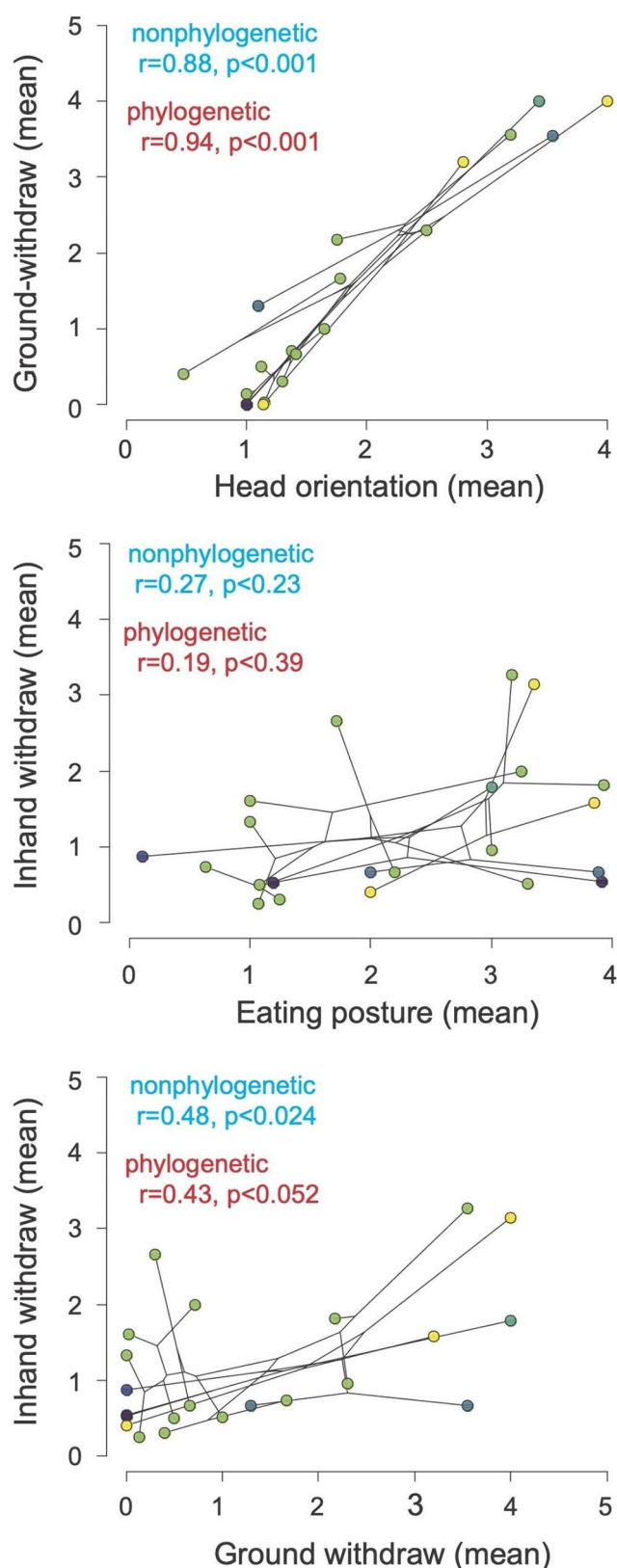
Figure 1 gives the proportion of food items that were initially either picked up with a hand or picked up with the mouth and then transferred to a hand. A few species displayed relatively few food item pickups using a hand (e.g., *Microcebus murinus*, *Cheirogaleus medius* and *Propithecus coquereli*), whereas others displayed only hand food pickups (*Daubentonia madagascariensis*, *Hapalemur simus* and *Loris lydekkerianus*). The remaining species displayed more equal numbers of food pickups using either the mouth or a hand (see also Peckre, Fabre et al. 2019).

### Relation Between the Four Withdraw Variables: Head Orientation, Ground-Withdraw, Body Posture and Inhand-Withdraw

Figure 2A describes the relationship between head orientation and ground-withdraw scores. We found a high correlation between the head orientation score (distance from the food item) and the ground-withdraw score (the contribution of the hand to the withdraw in getting a food item to the mouth) (Fig. 2A; non-phylogenetic correlation:  $\rho=0.88$ ;  $S=207.91$ ;  $p<0.001$ ; phylogenetic correlation:  $\rho=0.94$ ;  $S=93.53$ ;  $p<0.001$ ). The relative contribution of the head and the hand to the withdraw movement (i.e. ground-withdraw score) depended on how near the head was to the food item as it was grasped (i.e. head orientation score). For example, if an animal was sniffing a food item as it was grasped, the hand contribution to the withdraw was small, whereas if an animal was reaching with an extended arm as the food item was grasped, the hand made a large contribution to getting the food to the mouth. Many species inspected the food by sniffing, and when sniffing, some concomitantly grasped the food with a hand. When the hand grasped a food item as it was being sniffed, the hand contribution to the withdraw movement was minimal because the mouth and the hand grasping the food were close to one another. This was common, for example, for the aye-ayes (*Daubentonia madagascariensis*). Another pattern observed was for the individual to sniff the food and then



**Fig. 1** Food items picked up by hand as a per cent of all food items that were handled with ground-withdraw or inhand-withdraw. Note: some species picked up all food items by hand (e.g., *Daubentonia*), others picked up most food items by mouth for transfer to a hand (e.g., *Microcebus murinus*), whereas still others displayed almost equal numbers of initial ground-withdraw and mouth pickups (*Eulemur albifrons*)



**Fig. 2** Correlations between (A) head orientation and ground-withdraw scores, (B) body posture and inhand-withdraw scores and (C) ground-withdraw and inhand-withdraw scores

withdraw the snout, with a hand subsequently advancing to grasp the food. With this pattern, common among Lemuridae species, the hand made a greater contribution to getting the food to the mouth. Other species appeared to visually identify food from a distance, or if they had sniffed the food, to subsequently withdraw the head so that they reached the item from a distance. For these species, the withdraw movement was mainly a movement of the hand (e.g., *Hapalemur simus*, *Loris lydekkerianus*). Food items that were picked up by hand from the ground were always immediately brought into contact with the snout/mouth by all individuals.

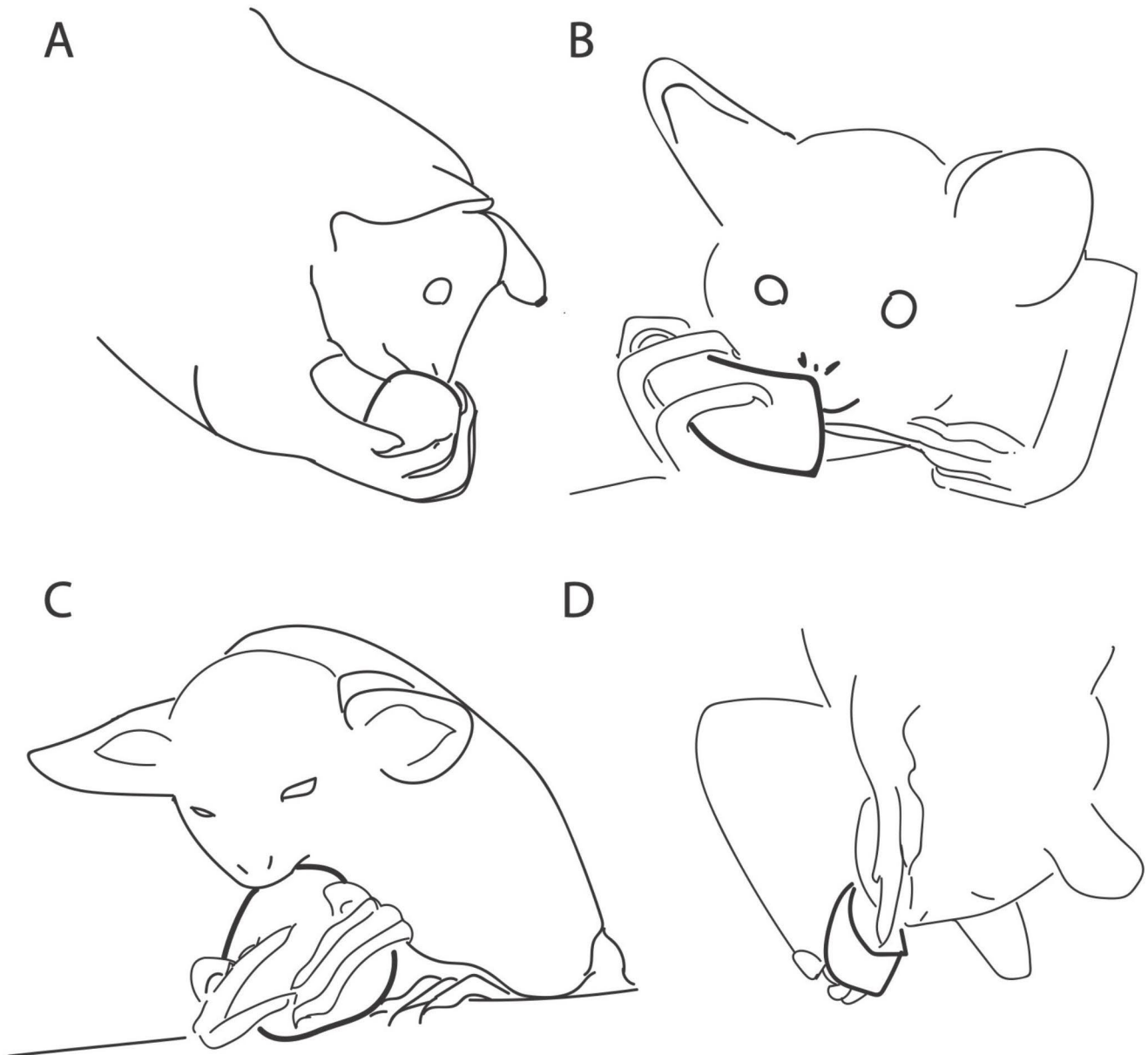
Figure 2B describes the relationship between body posture and inhand-withdraw scores. It was expected that if an animal sat in an upright position at some distance from the food, the contribution of the hand to the withdraw movement would be greater than if the animal crouched over the food. Nevertheless, there was no significant positive correlation between body posture scores and inhand-withdraw scores (Fig. 2B;  $\text{rh}\hat{=}0.27$ ;  $S=1296$ ;  $p=0.227$ ; phylogenetic correlation:  $\text{rh}\hat{=}0.19$ ;  $S=1240$ ;  $p=0.396$ ). The absence of a correlation occurred because all species often made reaching movements toward the food with the mouth rather than a hand, both when sitting in an upright position or when hunched over the food that they were holding. In addition, some of the species readily reached with the mouth for quite long distances when taking food from the hand (e.g. *Propithecus coquereli*), perhaps enabled by their neck length.

Figure 2C describes the relationship between ground-withdraw and inhand-withdraw scores. Species for which the hand poorly contributed to the withdraw when picking up the food on the ground also made more use of head movements to reach food in the hand. This significant positive non-phylogenetic correlation (Fig. 2C;  $\text{rh}\hat{=}0.48$ ;  $S=921.71$ ;  $p=0.024$ ) is influenced by the presence of two clusters: a tight cluster of species with low scores on both measures (e.g. *Microcebus murinus*, *Cheirogaleus medius*, *Nycticebus coucang*, *Daubentonia madagascariensis*, *Eulemur rubriventer*, *Eulemur coronatus*) and a more diffuse cluster of species with high scores on both measures (e.g. *Hapalemur simus*, *Hapalemur griseus*, *Loris lydekkerianus*, *Nycticebus pygmaeus*, *Propithecus coquereli*). The phylogenetic structure of this effect is confirmed by the absence of a significant phylogenetic correlation ( $\text{rh}\hat{=}0.43$ ;  $S=874$ ;  $p=0.052$ ).

## Species-Typical Withdraw Movements

### Daubentoniidae

A total of 25 food item pickups consisting of pieces of melon, apple and banana were obtained from *Daubentonia madagascariensis*. All pickups were made with a hand, and

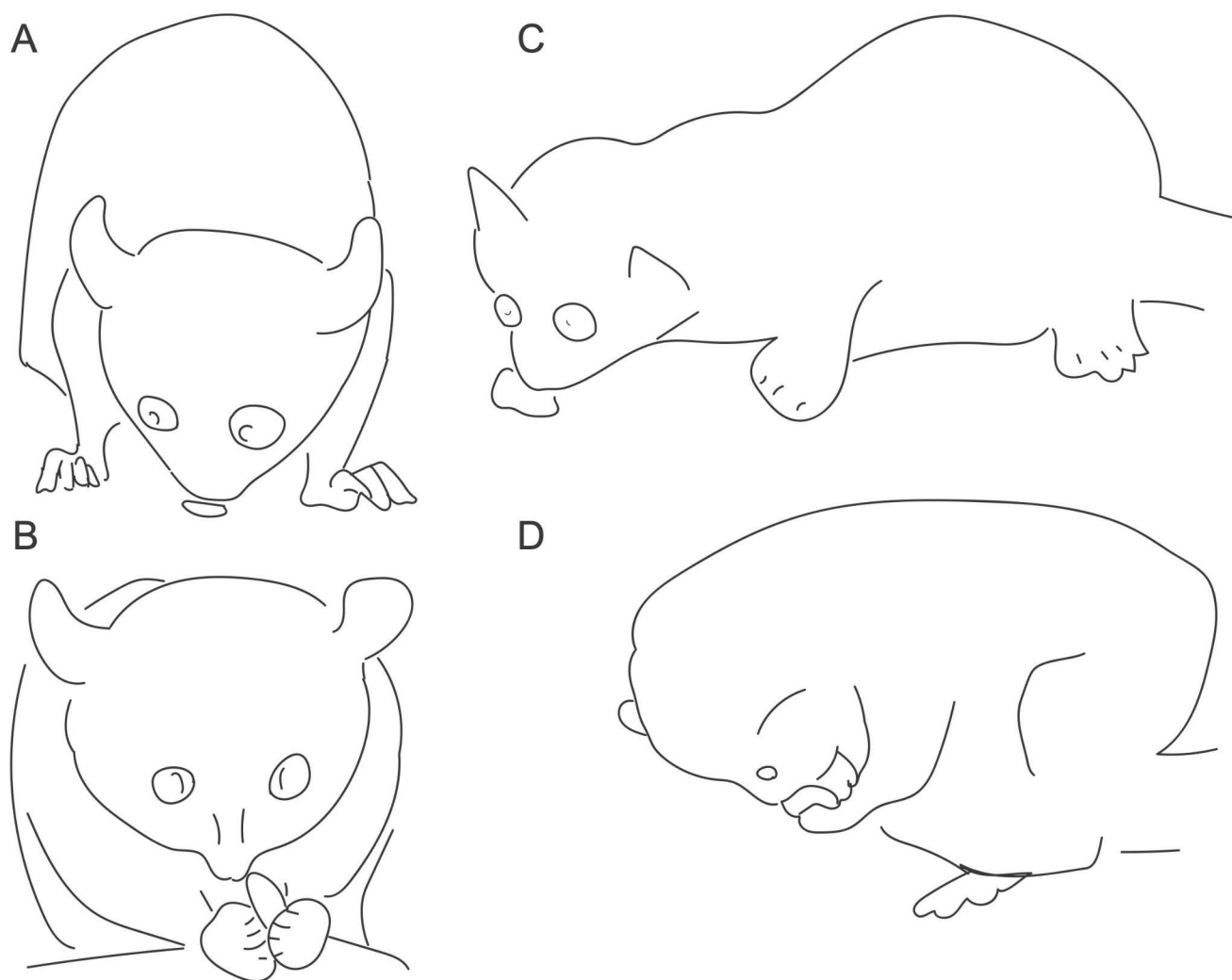


**Fig. 3** *Daubentonia madagascariensis* (A) making a ground-withdraw grasp with the nose juxtaposed to the food target (apple), (B) withdrawing the contents of a banana with 3rd digit fishing movements while draped over a branch with the branch supporting the chest, (C)

for all pickups, the nose was oriented near the food item as the item was grasped with a hand, giving a low average ground-withdraw score ( $0 \pm 0$ ) showing low hand contribution (Fig. 3A). After grasping the food, the aye-aye always moved to a nearby perch to eat. There were 55 occasions where the individual raised its head away from the food held in the hand, allowing for the subsequent scoring of 55 inhand-withdraw movements. On these occasions, the snout moved toward the food that was held in a relatively stationary hand, giving an average inhand-withdraw score signifying almost no hand contribution to the withdraw

sitting on a pole biting at an apple that is supported by the pole and held in both hands, and (C) fishing with the 3rd digit for the contents of a melon while hanging from the hind feet

( $0.88 \pm 0.30$ ). When eating food from the hand, the aye-aye adopted a variety of eating postures, including being draped over a bar with the bar supporting the chest (Fig. 3B), sitting on a bar with the elbows also resting on the bar (Fig. 3C), or hanging by the hind feet (Fig. 3D). When the aye-ayes were so positioned, two kinds of eating behavior were observed. With pieces of apple, the animals mainly held the item with both hands and licked, sucked, and nibbled for long periods of time without moving their head away from the food item (Fig. 3C). With pieces of banana still enclosed in the banana peel and with pieces of melon, they held the food item in



**Fig. 4** Comparison of two species of *Cheirogaleidae*. (A) *Cheirogaleus medius* stands with a wide base of support and (B) picks up by mouth a food item that is held in both hands as the animal adopts an upright sitting posture. (C) *Microcebus murinus* stretches out its neck (D) to

pick up by mouth a food item that is held in both hands for eating as the animal adopts a hunched over sitting posture. Note: the location of a food item relative to the mouth does not require visual guidance

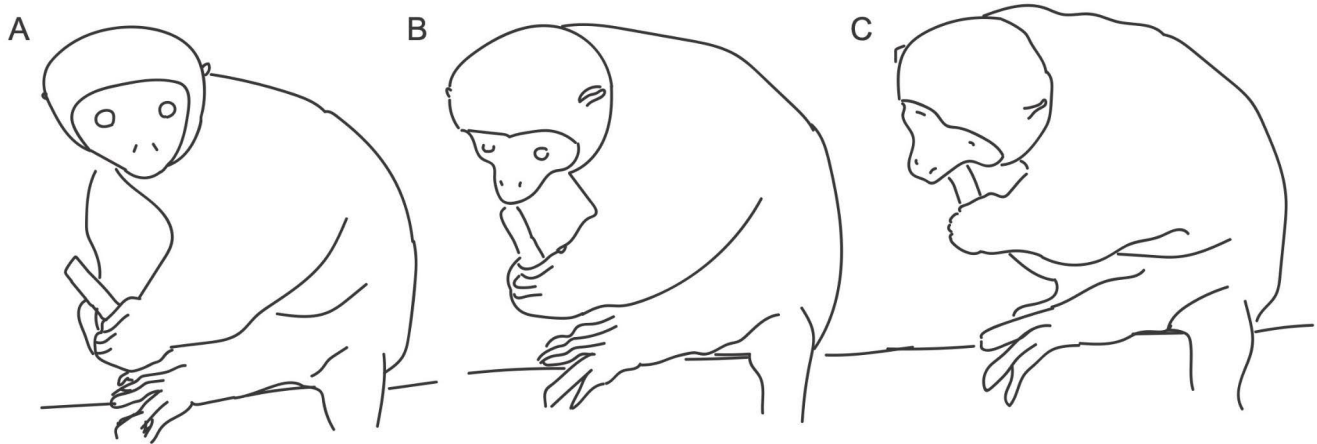
one hand and fished for pieces of the fruit with in-out movements of the long third digit of the other hand (previously reported in Lhota et al. 2009). The fishing behavior consisted of many consecutive movements with a rate of 2 to 4 per second, in which the fingertip was inserted into the fruit and retracted into the adjacent mouth (Fig. 3B). Occasionally the fishing withdraw movements would pause while the animal licked its third digit. Because of its idiosyncratic withdraw strategy, in which the animals seldom adopted a sitting posture and were either in a horizontal or upside-down position, head orientation and body posture average scores were low ( $1 \pm 0$  and  $0.11 \pm 0.05$ , respectively).

### Cheirogalidae

Similar to *Daubentonia* both *Cheirogaleus medius* (observed picking up 32 food items) and *Microcebus murinus* (observed picking up 45 food items) picked up all food items using the mouth, giving head orientation and ground-withdraw scores of 0 and 0.

When picking up food items with the mouth, *M. murinus* adopted a quadrupedal stance, with the forelimb placed in a wide stance and with the head extended to grasp a food item (Fig. 4A). Once a food item was picked up with the mouth, *M. murinus* reached and took the food from the mouth and held it in the hands for subsequent eating. When taking a food item from the mouth, both hands reached for the item almost simultaneously. For reaching, the hands were oriented with the palm in a perpendicular position from which





**Fig. 5** *Propithecus coquereli* (A) holds a carrot in both hands while in a sitting posture, (B) makes an inhand-withdraw to bring the protruding end of the carrot to contact the tip of the mouth and (C) adjusts its

head position and carrot position to bite using its molars. Note: the animal contacts the carrot using perioral receptors before positioning the carrot for biting

they were moved to the food with an elbow-in movement. With the food held in the hands (Fig. 4B), *Microcebus murinus* adopted a sitting, upright oblique posture (average body posture score of  $3.92 \pm 0.08$ ).

*C. medius* also picked up food items in the mouth but extended its head to do so (Fig. 4C), and they reached and took the food from the mouth as they adopted a sitting posture. The sitting posture adopted for eating was one in which they were hunched over the food (Fig. 4D), with the food item held on the substrate or with the elbows resting on the ventrum (average body posture score of  $1.19 \pm 0.34$ ), postures that resulted in the mouth usually reaching to take food from the hand.

Hence, the bimanual food-holding strategy adopted by both cheirogaleid species resulted in most of the movement of reaching for the food held in the hand being performed by movement of the mouth to the food, giving low average inhand-withdraw scores (*Microcebus murinus*:  $0.54 \pm 0.17$ ; *Cheirogaleus medius*:  $0.53 \pm 0.00$ ).

### Indriidae

*Propithecus coquereli* were observed reaching for 63 food items placed on a horizontal surface, and they were also observed eating leaves (16 branches and 86 reaching events). When reaching for food items on a shelf, the animals reached for nearly all food items with their mouth (57 of 63 items). When reaching for food from the substrate, the hands usually grasped the cage wall or other objects in the cage for support, and the individuals extended their long necks to reach items even from a distance. When eating leaves, the animals reached for a branch and then held the branch relatively still with one hand as they reached for the leaves to take them with their mouth. Only 7 ground-withdraw movements to pick up food items using a hand

were observed, all from one of the six animals. This gave an inflated ground-withdraw score relative to all of the food items obtained. The reaches made by this individual were made from a distance, and the withdraw mainly involved the hand coming to the mouth with the food items adjusted to be placed in the mouth after first contacting the mouth (average ground-withdraw score of  $4 \pm 0$ ).

For inhand-withdraws ( $n=197$ ), the animals adopted a sitting posture with the back in an oblique orientation and with the lower arm extending at about a  $90^\circ$  angle from the vertically held upper arm (average body score of  $3 \pm 0$ ). Inhand eating mainly involved head movements toward the food accompanied by minimal orienting of the hand, giving a low average inhand-withdraw score ( $1.78 \pm 0.30$ ). Figure 5 illustrates the sitting posture of an animal holding a carrot (Fig. 5A) and the relatively large head movement toward the carrot (Fig. 5B). The carrot was not taken directly into the mouth but was first contacted by mouth, only then to be positioned to the side of the mouth for biting with the molars (Fig. 5C).

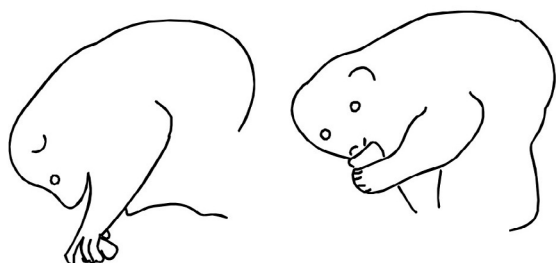
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### Lemuridae

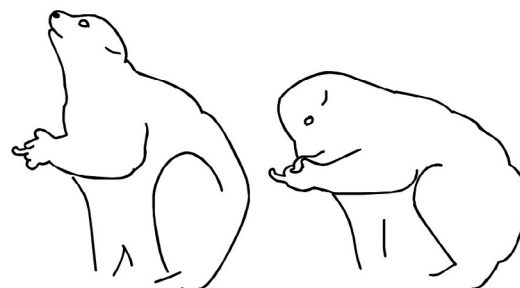
For analysis, we divided the Lemuridae into two phylogenetic groups, (1) the Eulemurinae (*Eulemur*) and (2) the other subfamilies comprising both the Vareciinae (*Varecia*) and the Lemurinae (*Lemur* and *Haplemur*).

The results of the scoring of eight species of *Eulemur* are summarized in Fig. 6. In all, 541 ground-withdraw movements (mean of 60 per species) and 2396 inhand-withdraws movements (mean of 266 per species) were scored. The most frequent ground-withdraw movements featured first advancing the nose toward the target object, then grasping the object by hand, and subsequently using the mouth to take the food item from the hand. For many species, the nose was

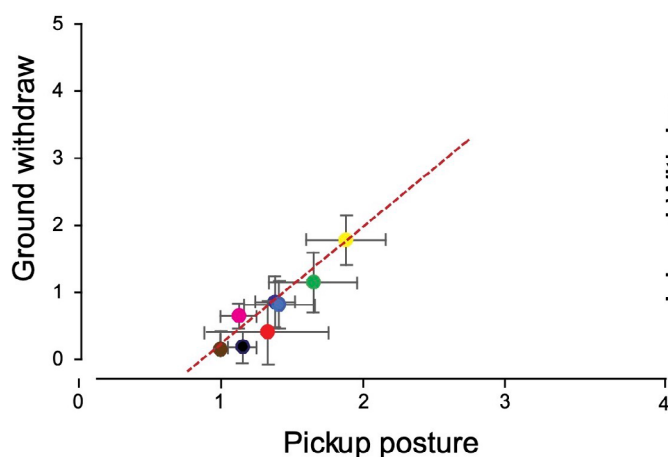
## A. Ground Withdraw



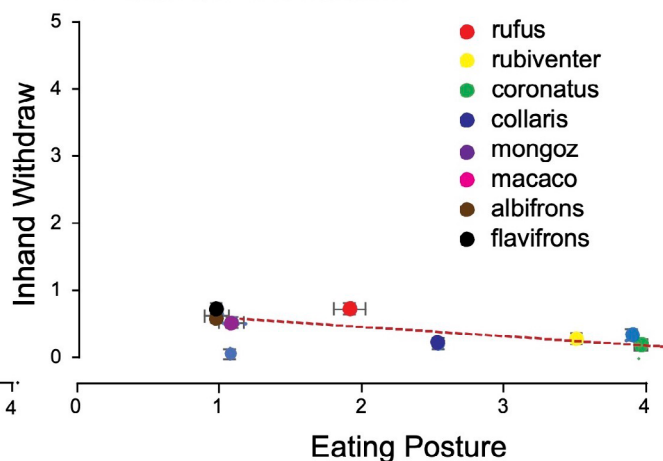
## C. In-hand Withdraw



## B. Eulemur correlation



## D. Eulemur correlation



**Fig. 6** Summary of results from 8 species of *Eulemur*. (A) *Eulemur rubriventer* illustrates head orientation and ground-withdraw as a food item is grasped; (B) relation between all *Eulemur* species orientation and ground-withdraw scores. (C) *Eulemur rubriventer* illustrates eat-

ing posture and inhand-withdraw; (D) relation between all *Eulemur* species eating posture and inhand-withdraw scores. Note: a high score for both posture and withdraw would signify an animal sitting upright with the hand transporting a food item to the mouth

proximate to the target object when it was grasped by the hand, but for some species, the distance of the nose from the target varied as indicated by the average head orientation scores ranging from  $1 \pm 0$  to  $1.88 \pm 0.28$  (Fig. 6B). The cartoons in Fig. 6A illustrates the head orientation of *Eulemur rubriventer* for a ground-withdraw. The figure shows the nose proximate to a food item and being raised so that the hand could advance. The mouth then turns to meet the hand and take the food. Figure 6B summarizes the correlation between the average head orientation and ground-withdraw scores for eight of the *Eulemur* species, which gave a significant correlation ( $\rho = 0.84$ ,  $S = 13.58$ ,  $p = 0.009$ ), despite the generally low scores on both measures by all species. The correlation shows that although the nose was proximate to the food when it was grasped, different species might raise the nose slightly more than others to allow the hand to advance onto the food (average ground-withdraw scores ranging from  $0.03 \pm 0.23$  to  $0.71 \pm 0.38$ ).

The first cartoon in Fig. 6C illustrates a *Eulemur rubriventer* in a three-point sitting posture with an oblique back position and with its snout raised to swallow a food

item. The second cartoon illustrates the *Eulemur rubriventer* lowering its snout to take a bite of food from an item held in the hand, which supinates but does not advance to meet the snout. Figure 6D summarizes the relation between average body posture and inhand-withdraw scores for Eulemuridae ( $\rho = 0.06$ ,  $S = 78.97$ ,  $p = 0.888$ ). For most inhand-withdraws, the animals were in a sitting position but the eating posture used varied by species, with some animals using a three-point posture (the hand not holding the food positioned on the surface) and the others adopting a two-point sitting posture, and with some animals maintaining an eating posture with the back almost horizontal and others maintaining an oblique back position (average body posture scores ranging from  $1 \pm 0$  to  $3.30 \pm 0.21$ ). To retrieve the food from the hand, all species mainly directed their mouth to the food (average inhand-withdraw scores ranging from  $0.25 \pm 0.13$  to  $2.66 \pm 0.4$ ). Often the hand was held in a supinated position or else supinated on the approach of the mouth. The correlation between ground-withdraw scores and inhand-withdraw scores was not significant ( $\rho = -0.07$ ,



**Fig. 7** Differences in inhand-withdraw by two lemur species. (A) *Hapalemur simus*, a lemur that featured an upright three-point posture and an inhand-withdraw that made a large contribution to getting food

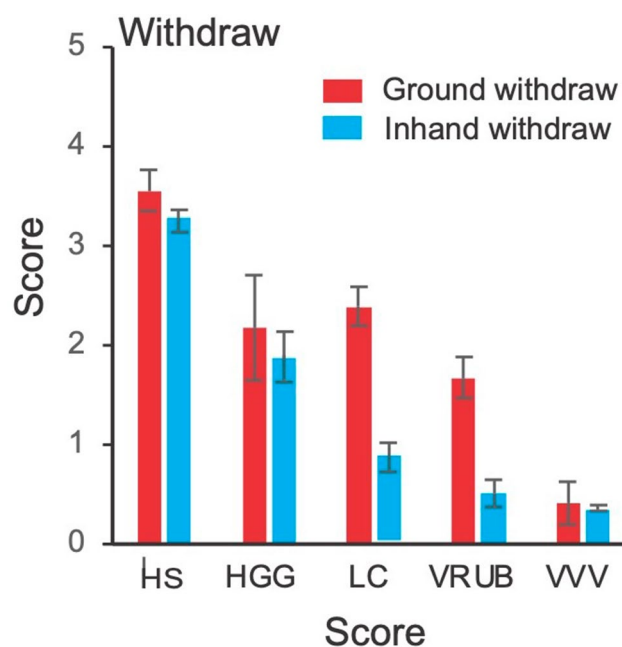
to the mouth. (B) The inhand-withdraw movement for *Varecia rubra* in which the head moves to the food and the hand makes little contribution to the withdraw

$S=90$ ,  $p=0.882$ ), contrary to the pattern observed when considering all species.

The five other lemur species were scored as they picked up 411 food items and made 1,332 inhand-withdraw movements (an average of 82 food items and 266 inhand-withdraws per species). Figure 7 summarizes the scores for these five lemur species, each of which displayed a different pattern of ground-withdraw and inhand-withdraw. The two *Hapalemur* species had high scores on both withdraw movements (ground-withdraw: *H.s.*  $3.55 \pm 0.21$  *H.g.*  $2.17 \pm 0.53$ ; inhand-withdraw: *H.s.*  $3.27 \pm 0.11$  *H.g.*  $1.82 \pm 0.27$ ). *Hapalemur simus* frequently made reaches from arm-length distance from a food item. They then withdrew the food item directly into the mouth. However, they visually disengaged the object as they grasped it, and it was only when the food

was brought into contact with the mouth that the item was oriented for biting. Furthermore, the inhand-withdraw movements involved no visual attention toward the hand during the withdraw. Figure 8 A illustrates the body posture and inhand-withdraw movement for *H. simus*, which reached from an upright three-point posture resulting in an inhand-withdraw where the hand made a large contribution to getting food to the mouth. Online Resource 1 shows a representative inhand-withdraw by *Hapalemur griseus*, in which kernels of corn are taken from a cob but with the cob only rotated to present the kernels to the mouth in response to mouth contact.

*Lemur catta* made more use of the hand for ground-withdraw ( $2.3 \pm 0.2$ ) and more use of the mouth for inhand-withdraw ( $0.95 \pm 0.15$ ), whereas the two *Varecia* species



**Fig. 8** Ground-withdraw and inhand-withdraw scores for five lemur species

had low scores for both ground-withdraw and inhand-withdraw movements (ground-withdraw: *V.v.*  $0.4 \pm 0.21$  *V.r.*  $1.67 \pm 0.21$ ; inhand-withdraw: *V.v.*  $0.3 \pm 0.03$  *V.r.*  $0.73 \pm 0.14$ ). Figure 8B illustrates the body posture and inhand-withdraw movement of *Varecia rubra*, a lemur that frequently rested the hands holding the food on the floor and reached for the food with the mouth.

#### Lorisidae

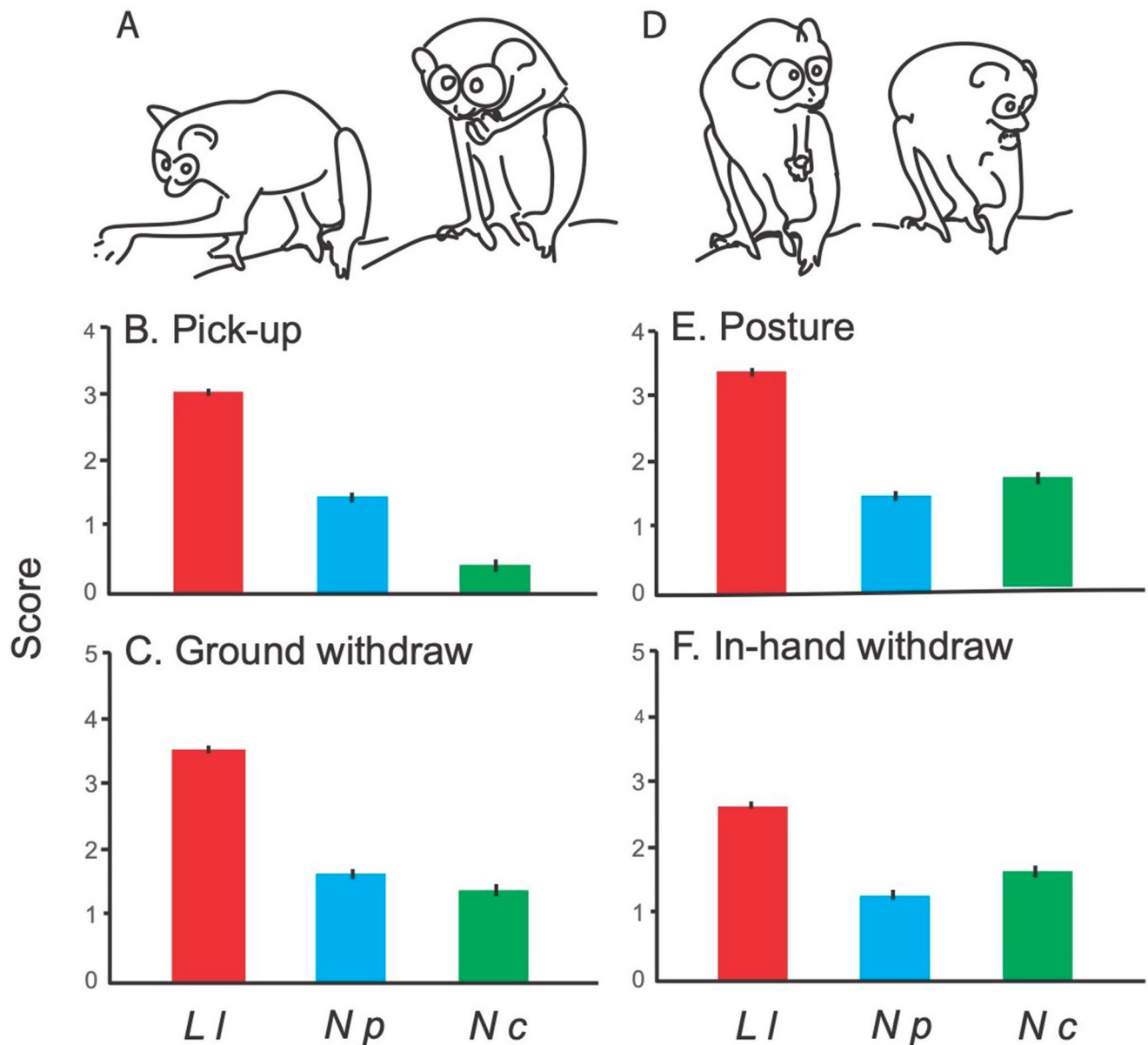
A summary of behavioral rating scores for *Loris lydekkerianus*, *Nycticebus coucang* and *Nycticebus pygmaeus* is shown in Fig. 9. Measures were obtained from 209 food item pickups that provided 417 inhand-withdraw movements from three loris species (averages of 70 and 139 per species). The behavior of *L. lydekkerianus* was different from the other two species. *L. lydekkerianus* nearly always used a single hand to pick up a food item and did so at a distance after making a few orienting (lateral and back and forth) head movements to fixate the target (average head orientation score of  $4 \pm 0$ ). Its ground-withdraw movements brought the food item to the snout with little concomitant head movement (average ground-withdraw score of  $4 \pm 0$ ). After an item contacted the snout, it was either discarded, or the animal sat back with the item still in its hand to eat (average body posture score of  $3.36 \pm 0.13$ ). When in a sitting posture, the loris did make head-turning movements to take the food item from its hand into its mouth, and so it received lower inhand-withdraw score than ground-withdraw score ( $3.14 \pm 0.1$ ).

*Nycticebus coucang* and *Nycticebus pygmaeus* were more likely to pick up food items with the mouth and then transfer the items to one or both hands for holding for eating (average head orientation score of  $1.14 \pm 0.14$  and  $2.8 \pm 0.26$  respectively). Both species used head movements to retrieve the food from the hand (average inhand-withdraw scores of  $0.4 \pm 0$  and  $1.58 \pm 0.21$ , respectively), but their body posture was different. *N. pygmaeus* would sit to eat in a three-point or two-point posture with the back in an oblique orientation (average body posture score of  $2 \pm 0$ ). *N. coucang* held its elbows against the torso and arched its head underneath its torso to retrieve food from the hand with the mouth (average body posture score of  $3.85 \pm 0.9$ ).

#### Galagidae

Data were obtained from two species of Galagidae, *Otolemur crassicaudatus* (18 food items and 74 inhand-withdraw observations) and *Galago senegalensis* (302 food items and 279 inhand-withdraw observations). *Otolemur* made all food pickups by mouth (average ground-withdraw score of 0), whereas *G. senegalensis* made about half of its pickups by mouth and the others by hand (average ground-withdraw score of  $3.55 \pm 0.31$ ). Even when picking up food by hand, *G. senegalensis* made orienting movements of the nose so that the target food item was almost touched, but it often then sat back and reached for the food by hand (average head orientation score of  $3.55 \pm 0.31$ ). Figure 10 summarizes inhand-withdraw movements and body posture of the two galagidae. *G. senegalensis* distinguished nonlive and live food items by sniffing nonlive food items and often taking them by mouth while reaching for live mealworms that they withdrew directly to the mouth. Again, once the hand reached the mouth, a food item was not taken directly into the mouth but was first positioned using perioral contact. The movement of the mealworm protruding from the hand would have made it impossible for them to predict the mealworms' accurate placement in the mouth.

The body posture of *Otolemur* involved sitting on the haunches with the torso horizontal (Fig. 10A; average body posture score of  $2 \pm 0$ ). The body posture of *Galago* consisted mainly sitting on the haunches holding food items in one or both hands with the torso oblique (Fig. 10B; average body posture score of  $3.89 \pm 0.11$ ). For both species, inhand-withdraw consisted mainly of the mouth orienting to the food item giving low scores for inhand-withdraw (Fig. 10C; average inhand-withdraw scores of  $0.66 \pm 0.26$  for *O.c.* and  $0.66 \pm 0.29$  for *G.s.*). When making inhand-withdraw movements, perioral contacts seemed to facilitate food transfer to the mouth.

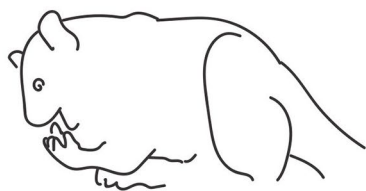
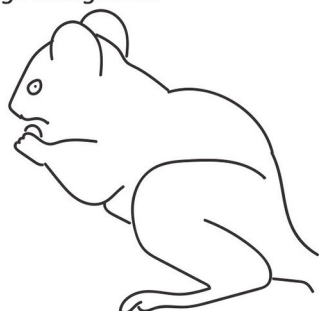


**Fig. 9** Ground-withdraw and inhand-withdraw for three species of Lorisidae. (A) *Loris lydekkerianus* makes a ground-withdraw in which most of the movement is made by the hand. (B) Orient scores and (C) ground-withdraw scores for three Lorisidae species. (D) *Loris lydekkerianus* features a 3-point oblique sitting posture from which both the head and hand contribute to the withdraw. (E) Eating posture and (F) inhand-withdraw scores for three Lorisidae species

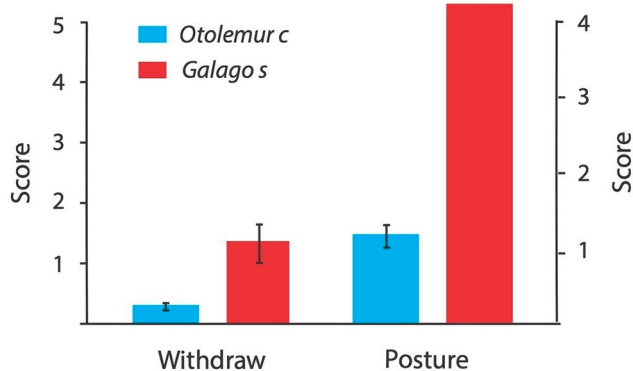
### Comparison of Species with High Ground-Withdraw Scores

The species with the highest ground-withdraw scores were *L. lydekkerianus* (average score of  $4 \pm 0$ ), *G. senegalensis* (average score of  $3.55 \pm 0.31$ ) and *H. simus* (average score of  $3.2 \pm 0.21$ ). A representative ground-withdraw by *L. lydekkerianus* is shown in Online Resource 2. In the video, the individual does reach out to almost touch the target food item with its nose, but after this movement is completed, it then reaches for and grasps the target by hand. It does not

take the food item into the mouth, but after sitting back, it sniffs the food and only then takes a bite. A representative ground-withdraw with a captured mealworm is shown in Online Resource 3 for *G. senegalensis*. The reach is made from a distance, and the mealworm is brought directly back to the mouth but only taken into the mouth after contact. A representative ground-withdraw followed by an inhand-withdraw is shown for *H. simus* in Online Resource 4. The food item is visualized as the reach begins but disengaged before the grasp is completed. The withdraw brings the food item to the front of the mouth, but then the item is moved

A. *Olemur crassicaudatus*B. *Galago senegalensis*

C. Galagidae: Inhand Withdraw



**Fig. 10** The eating posture of two species of Galagidae. (A). *Otolemur crassicaudatus* sitting posture was on the haunches with the torso horizontal. (B). *Galago senegalensis* sitting posture was on the haunches holding food items in one or both hands with the torso oblique. (C) For both species, inhand-withdraw consisted mainly of the mouth orienting to the food item giving low scores for movement of hands during the withdraw

to the side of the mouth for biting with the molars. For the inhand-withdraw, the hand and the head make almost equal contributions, and the food is taken into the mouth following perioral contact.

## Discussion

This study investigated the contribution of vision to the withdraw movement to transfer food from a hand to the mouth in strepsirrhine primates. Withdraw movements were examined during normal feeding in captive animals comprising 22 species from six families. Rating scales evaluated head orientation, body posture and the use of the hand in

two types of withdraw movements. The assumption underlying the analyses is that, if vision contributed to the withdraw of a food item, that would be signified by the behavior of looking at the item grasped in the hand to guide it for subsequent accurate placement in the mouth. The results gave no indication of the use of vision for guiding the withdraw movement in any strepsirrhine species.

The evidence that anthropoid primates use vision to guide the withdraw movement of bringing food to the mouth is that they look at a food item as it is grasped, adjust the orientation of a food item in the hand, and then accurately place the item into the mouth where it is taken with a single bite (Hirsche et al., 2022). There was no evidence that any strepsirrhine species used any of these strategies to get food into the mouth. The scores for head orientation, which quantifies the distance and orientation of the head relative to a food item that was to be picked up with a ground-withdraw movement, indicated that, for most species for most reaches, it was the nose that was brought proximal to the food item. This behavior suggests that olfaction and touch were contributing to item location and identification. Moreover, once snout/hand proximity was obtained when initially grasping food, it resulted in the item being transferred from the hand to the mouth almost immediately, a transfer that used touch and required no vision. The relative contribution of the head and the hand to the withdraw movement depended on how near the head was to the food item as it was grasped (high correlation between head orientation scores and ground withdraw movements). When food items were held inhand, most species oriented the snout to the food held in the hand and sniffed, touched, licked, or adjusted the position of food items by mouth, again suggesting the use of olfaction, taste, and touch. Species for which the hand poorly contributed to the withdraw movement when picking up the food on the ground also made more use of head movements to reach the food in the hand (correlation between ground withdraw and inhand withdraw scores). Taken together, these observations suggest that strepsirrhines use nonvisual cues to guide food items into the mouth. Many of these nonvisual strategies are used by non-primate animal species. For example, tree kangaroos (*Dendrolagus*) use tactile cues on the mouth in association with head movements to guide vegetation into the mouth from the hand (Iwaniuk et al., 1998), rodents use vibrissae cues and head movements to guide food to the mouth (Whishaw & Coles, 1996; Whishaw et al., 1998, 2018, 2020) and the gray short-tailed opossum (*Monodelphis domestica*) uses a wide-open mouth to receive a prey item from the hand (Ivanco et al., 1996).

Most of the strepsirrhine species adopted a sitting posture when handling and eating food. A sitting posture for eating is a featured posture in Euarchontoglires, including rodents, strepsirrhines, and anthropoids (Whishaw et al., 1998;

Reghem et al., 2011; Hirsche et al., 2022). Many strepsirrhine species also engaged in one-handed eating. The use of a sitting posture freeing the head along with one hand during eating could contribute to food visualization as it increases the degrees of freedom of movement by the head and the hand. However, there was no evidence that these eating postures resulted in animals adjusting the orientation of food that they held in their hand using vision. All species often made reaching movements toward the food with the mouth rather than a hand, both when sitting in an upright position or when hunched over the food that they were holding (no correlation between body posture score and inhand withdraw scores). Amongst the species that did sit upright and hold food in one hand, the food was always explored using perioral receptors before biting, suggesting that they used touch for food orientation. A few species preferentially used two hands to hold food (e.g., *Microcebus murinus*), hunched over their food (e.g., *Cheirogaleus medius*), or had an idiosyncratic eating strategy in which the mouth and food were always in close contact, (e.g., *Daubentonia*). These are strategies that hide the food from vision as it is taken by the mouth from the hand.

Previous studies of withdraw movements in macaques and humans have contrasted how small and large food items are transferred from a hand to the mouth. For small items grasped in the hand, touch perception of the object by the fingers provides the information necessary to accurately position an object in the mouth. Experimental studies with visually occluded humans show that the fingers can be accurately directed to targets on the body (Edwards et al., 2005), and the hand can accurately place a food item or take food from the mouth (de Bruin et al., 2008; Sacrey et al., 2011; Karl et al., 2012). If a food item is large and protrudes from the hand, however, and if the distal portion of the food is to be placed in the mouth, somatosensory information from the hand is insufficient to direct the distal end of the food item to a mouth target. Macaques and humans deal with protruding food items by focusing their eyes on its distal portion to calculate the trajectory of the item into the mouth (Hirsche et al., 2022; Whishaw et al., unpublished). An analysis of how the strepsirrhines dealt with food items of different sizes could not be similarly investigated. First, they had a propensity to pick up smaller items in the mouth, presumably because their whole-hand grasping strategies were not adequate for grasping small food items (Peckre et al., 2019). Second, all the large items that they did bring to the mouth with a hand were first touched to the mouth before being oriented for biting.

A surprising aspect of the behavior of the strepsirrhines was their olfactory investigation of food before they grasped it (see Nevo and Heymann 2015). Even species that often reached for food from an arm's length, including *Loris*

*lydekkerianus* and *Galago senegalensis*, often also advanced their nose in proximity to the food prior to reaching, suggesting that they were making some use of olfaction to identify food items. In this respect, it is interesting that *Galago senegalensis* reached from a distance for mealworms that were moving but usually sniffed other food items before reaching, suggesting that sniffing was not obligatory. Olfactory investigation may have occurred because a variety of foodstuffs were concurrently present at a feeding site, and the animals were searching for more favored food items. Nevertheless, the food that they were given was usual fare, so it might be expected that they would be able to visually identify preferred items.

A number of strepsirrhine species were notable for the way in which they used a hand for withdraw movements. *L. lydekkerianus* made more extensive use of the hand for ground-withdraw movements than did other strepsirrhines (see also Peckre, Fabre et al. 2019). Nevertheless, as did the other strepsirrhines, they did assist ground-withdraw movements by additionally reaching with the mouth. Although the versatile use of the hand by *L. lydekkerianus* has been noted previously (for a review, Nekaris 2005), there was no indication that they used vision to assist in their withdraw movement. *L. lydekkerianus* was notable in holding a food item adjacent to the snout for a considerable time after a withdraw, which along with the hand positioning movements they made near the mouth, suggested that they were using perioral cues to assist in food positioning.

Whereas color vision appears to characterize all diurnal catarrhines and platyrrhines, many strepsirrhine species are strictly dichromatic, and a few have polymorphic trichromacy in that only some females are trichromatic (Jacobs, 2015). Moreover, many of the strepsirrhine species have a single cone photoreceptor for short wavelengths of light, lack a dense photoreceptor region for detailed vision, and have 6 to 10 times less visual acuity than anthropoids. Taken together, deficient visual acuity may promote the use of nonvisual senses to assist with food discrimination (Kirk, 2004; Veilleux and Christopher Kirk 2009). It is interesting that in addition to these differences in the visual systems of strepsirrhines and anthropoid primates, strepsirrhines have a smaller agranular frontal cortex area than do anthropoids and may not have homologues to anthropoid neocortical areas 9, 12/47, 46 and 10. These are frontal lobe regions involved in object and spatial working memory of the type that might be required for visually-based food size and orientation calculations (Preuss & Goldman-Rakic, 1991; Goldman-Rakic, 1992). Thus, the feeding behavior of strepsirrhines may be influenced not only by constraints via visual receptors but also by cortical regions that support visual perception.

There were differences in the incidence and the form of food retrieval and withdraw behavior within and between strepsirrhine families. Phylogenetic analysis showed that there was only a weak relationship between families and species on the measures of posture and withdraw. One species of a family would sit nearly upright to eat, whereas another hunched over. One species of a family might pick up food by mouth, and another species of the same family might pick up food by hand. Species that made the most use of the hands included insectivores and folivores, suggesting that similar strategies are usefully applied to a variety of foods. Mobile food items (e.g. insects) were shown to involve increased use of the hand compared to immobile food items in strepsirrhines (Peckre et al., 2019). *G. senegalensis* reached directly for live mealworms by hand while first sniffing the immobile items. In both cases, the item, once grasped was not taken directly into the mouth but was first positioned using perioral contact. These results suggest that behavioral variation in strepsirrhine species was due mainly to feeding niche.

A caveat relevant to the methods used in the present study is that a definitive description of vision use in food handling would require the use of eye-tracking glasses. For humans, the use of eye-tracking glasses shows that the timing and duration of food visualization are related to orienting food for withdrawal to the mouth (de Bruin et al., 2008; Sacrey et al., 2011). The same studies report that after visualizing food for orientation, the subjects blink as they disengage, as do macaques (Hirsche et al., 2022). This blinking can be taken as a sign of “attentional” relaxation after a period of gaze anchoring on a food item. There was no evidence that any of the strepsirrhines blinked in conjunction with any portion of the withdraw. Future work could use eye-tracking glasses to confirm that the withdraw strategies used by strepsirrhines were nonvisual. The methodology of the present study was also opportunistic, as the animals were eating their usual fare. Future work could designate small and large food items in a more definitive experimental design. For example, *L. lydekkerianus* has been reported to pick up some items as small as ants (Nekaris, 2005), but no such food items were used here. Finally, some aspects of the withdraw movement, such as the reorienting of food as it contacted the mouth, were difficult to describe from the few video frames in which the behavior occurred, so future work could use higher frame rate video recording.

In conclusion, an extensive examination of thousands of withdraw movements made by strepsirrhines provided no evidence that any species used vision to assist in withdrawing food items by hand for placement in the mouth. It is likely that the visual mediation of food orienting for

placement in the mouth during the withdraw movement is an anthropoid innovation. Moreover, the observations did reveal that strepsirrhines are extremely versatile in using their hands to get food to the mouth despite their varied diets. The present findings are consistent with the idea that the evolution of the visual control of feeding was not a singular event but evolved in stages along with many other enabling behavioral and physical modifications associated with visual guidance of hand movements.

#### Online Resource captions.

**ESM 1** Inhand-withdraw by *Hapalemur griseus*. Uneaten kernels of corn are identified using perioral contact.

**ESM 2** Ground-withdraw by *Loris lydekkerianus*. The individual does reach out to almost touching the target food item with its nose, but after this movement is completed, it reaches for and grasps the target by hand. It does not take the food item into the mouth, but after sitting back, it sniffs the food and only then takes a bite.

**ESM 3** A ground-withdraw with a captured mealworm by *Galago senegalensis*. The reach is made from a distance, and the mealworm is brought directly back to the mouth but only taken into the mouth after contact.

**ESM 4** Ground-withdraw followed by an inhand-withdraw by *Hapalemur simus*. The food item is visualized as the reach begins but disengaged before the grasp is completed. The withdraw brings the food item to the front of the mouth, but then the item is moved to the side of the mouth for biting with the molars. For inhand-withdraw, the hand and the head make almost equal contributions, and the food is taken into the mouth following perioral contact.

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#### Declarations

**Competing interests** The authors declare no competing interests.



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