

Food acquisition on arboreal substrates by the grey mouse lemur: implication for primate grasping evolution

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Abstract

The use of the hand in food grasping is a shared characteristic of primates. However, the factors involved in the elaboration of this function remain unclear. Grasping hands may have evolved in an arboreal habitat with narrow branches. Interestingly, grasping may also have an association with different types of feeding such as insect predation, fruit and flower exploitation, or both. No study has tested the importance of substrate diameter and food properties on the use of the hand in food grasping. Yet, both of these parameters likely impose important selective pressures on the origin and evolution of manual grasping strategies in the context of food acquisition. Here, we quantified whether (1) substrate diameter (narrow, wide) and (2) food properties (static, slow moving, fast moving) influence food grasping in a small primate, *Microcebus murinus*. Our results show that narrow substrates increase the use of hands in prey grasping. The mouth is preferentially used to grasp static food (banana), whereas the hands are preferred to grasp moving prey (mealworm and cricket) regardless of the substrate. Thus, the narrow branch niche may be an important selective pressure on the emergence of manual food grasping in primates, but predation likely also played a key role.

Introduction

Among many other features, primates are characterized by a clawless grasping hand used both for moving on arboreal substrates and for grasping food items. Even if numerous non-primate species use also the hand to grasp substrates during arboreal locomotion, very few use it in food acquisition, whereas all the primates do so. Moreover, a wide diversity of manual grasp types exists among primates (Bishop, 1964; Christel, 1993; Pouydebat *et al.*, 2009). Yet, the factors involved in the evolution of manual grasping in the context of food acquisition in primates remain unclear. Many authors consider the exploitation of an arboreal niche of narrow branches at the root of the primate tree (Ravosa & Dagosto, 2007; Ross & Martin, 2007) and others associate foraging to the development of prehensile hands (Cartmill, 1972, 1974a,b; Rasmussen, 1990; Godinot, 1991, 2007; Sussman, 1991). In the context of this framework, several hypotheses exist. Firstly, the visual predation hypothesis suggests that the prehensile hands of primates with long and clawless fingers were originally an adaptation for locomotion on narrow branches and were used subsequently for visually guided manual predation on insects (Cartmill, 1972, 1974a,b; Kirk *et al.*, 2003). Secondly, the angiosperm exploitation hypothesis suggests that these traits are also correlated with exploitation of narrow branches but with a visually guided grasping of fruits

and flowers rather than insect predation (Sussman, 1991). The grasping extremities would be adapted to move among the tips of narrow branches to get hold of small fruits and flowers. Thirdly, Rasmussen (1990) combines these hypotheses considering the narrow branch niche in which the first primates foraged for both fruits and insects. Finally, Godinot (1991, 2007) suggested that the primate hand with long and clawless fingers would be more adapted for insect predation than for the use of narrow branches. This specialization for insect predation consists of jumping onto the prey and grabbing hold of it with the hands while remaining attached by the feet on the branch (Charles-Dominique, 1977; Niemitz, 1984; Godinot, 1991). According to Godinot (1991), this specialization is consistent with long fingers, which enhance the surface for catching prey, and the broadened distal parts of the finger, which enhance a stable grasp. Several extant non-primate species such as *Caluromys* and *Ptilocercus* are adapted to the narrow branch niche and show long fingers and prehensile hands, but do not possess nails (Sargis, 2001; Schmitt & Lemelin, 2002). Moreover, although these species are able to catch insects with their hands, they are not specialized as mentioned above. Although these authors all suggest that the grasping clawless hand of primates would have arisen in correlation with functional demands, the ecological context of the use of the hand in food grasping thus remains poorly understood.

Food properties have been shown to influence the use of the hands in grasping for primates and non-primates alike (Castiello, Bennett & Paulignan, 1992; Ivanco, Pellis & Whishaw, 1996; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009). One or both hands are typically used to catch fast-moving foods (e.g. insects), particularly in platyrrhines, strepsirhines, rats and opossums (Petter, 1962; Martin, 1972a,b; Charles-Dominique, 1977; Niemitz, 1984; Ivanco *et al.*, 1996; Nekaris, 2005). Yet, many of these animals preferentially use the mouth to grasp static food such as fruit (Rothe, 1971; Pollock, 1977; Singer & Schwibbe, 1998; Whishaw, Sarna & Pellis, 1998; Reghem *et al.*, 2011; Scheumann *et al.*, 2011). However, the substrate used during food grasping is rarely considered in this context and whether the substrate actually influences grasping strategies remains unknown.

In this study, we test the influence of both substrate diameter and food properties on the grasping strategies used by *Microcebus murinus* (Strepsirhini, Cheirogaleidae). This species is often viewed as a good model to represent the behaviour and ecology of basal primates (Martin, 1972a,b; Cartmill, 1974a,b; Crompton, 1995; Gebo, 2004). Indeed, a small-sized, generalist, omnivorous and nocturnal animal exploiting a narrow branch niche such as *M. murinus* was proposed to adequately describe the first primates (Martin, 1972b; Charles-Dominique, 1977; Gebo, 2004). The narrow branch niche described for *M. murinus* and for the first primates consists of branches of small diameter relative to the size of the animal, allowing the fingers to completely close around these substrates (Gebo, 2004; Dagosto, 2007). During food grasping, *M. murinus* uses its mouth in high proportion for small static food items like pieces of fruit (Ward & Hopkins, 1993; Reghem *et al.*, 2011; Scheumann *et al.*, 2011), but demonstrates an increase of hand use while catching prey in the wild (Martin, 1972a,b; Charles-Dominique, 1977; Siemers *et al.*, 2007). In this study, we test the corollaries of the four major hypotheses on primate origins outlined above by exploring whether grasping strategies are affected by substrate diameter (wide and narrow) and food properties (static: banana, slow moving: mealworms and fast moving: crickets). Consequently, we tested whether and how these factors may have played a role in the hand use in food grasping.

Firstly, we predict that substrate diameter will have an influence on stability and thus on grasping strategy. The narrow diameters should result in an increase of the use of the hand in food grasping. Indeed, *M. murinus* being a specialist of narrow branches and possessing a powerful pedal grasp should be more stable on narrow substrates rather than on wide ones. Secondly, we suggest that static food grasping likely involves fewer constraints in contrast to the grasping of moving prey. For stationary food items, animals can use the mouth to grasp it while maintaining hand and foot contact with the substrate (Reghem *et al.*, 2011; Scheumann *et al.*, 2011). However, to grasp a moving prey successfully, the use of the mouth is likely less efficient in animals having the choice to use a prehensile organ (e.g. tongues in chameleons or frogs). Indeed, the use of a prehensile organ such as an arm or a tongue allows an animal to increase its range of effective prey

capture without needing to resort to whole body displacements, which may decrease balance and attract predators. Consequently, we predict that the presence of moving food should increase the use of manual grasping in animals that have strong prehensile feet and thus do not need to support their body with the front limbs at all times.

Material and methods

Species and husbandry

Microcebus murinus (Miller, 1777) is a small arboreal, nocturnal and omnivorous strepsirhine endemic to Madagascar (Martin, 1972a,b). This species is classified as a branch walker and runner and has been suggested to prefer to move on narrow horizontal substrates in the wild (Petter, 1962; Martin, 1972a). The individuals of the study were all born in the captive colony of the UMR 7179 of the Muséum National d'Histoire Naturelle (Brunoy, France, Agreement 962773). Their cages and the experimental enclosure were placed in a maintenance room recreating natural environmental conditions with a constant ambient temperature of 24–26°C and 55% humidity. The individuals were exposed to a 12-h light/dark cycle (night: 2:00 PM–2:00 AM; day: 2:00 AM–2:00 PM) and received foods and water *ad libitum*. The experimental protocols used here adhered to the legal requirements of the European Union and the American Association of Physical Anthropologists Code of Ethics.

Experimental set-up

Five adult males (age: 4 ± 1 years old; mass: 82 ± 2 g; mean \pm SEM) were filmed using two cameras (Sanyo X Acti Full HD 1920 \times 1080, Sanyo France, Gennevilliers, France) set at 30 fps. A wooden nest box was mounted inside in a transparent experimental enclosure (51 \times 25 \times 26 cm; Fig. 1) with a single horizontal substrate. Two substrate diameters were selected to obtain relevant, yet different constraints. As the precise diameter of the substrate used by the mouse lemurs in the wild is not known, we considered a narrow diameter as one where the hands and feet are able to wrap around the substrate. To determine the size of the substrates in our experiments, we measured the size of the hands and feet of eight individuals. To do so, we took pictures of the hands and feet flattened on a piece of Plexiglass. The mean (\pm SEM) palm length was 10.6 ± 0.2 mm; the length of the longest finger: 9.7 ± 0.2 mm; foot sole length: 12.8 ± 0.3 mm; longest toe length: 10.3 ± 0.3 mm. The narrow substrate used in this study was 2 mm in diameter or 6.3 mm in circumferences and thus narrower than the size of the hands and feet. We hypothesize that this diameter approximates the narrow branch milieu or narrow terminal branch niche used by mouse lemurs in the wild (Petter, 1962; Cartmill, 1972; Martin, 1972a; Rasmussen, 1990; Sussman, 1991). We characterized as a wide diameter one where the hands and feet are unable to close around the substrate. The wide substrate chosen measured 20 mm in diameter resulting in a circumference of 62.8 mm, larger than the length of the hand or foot plus longest finger or toe.

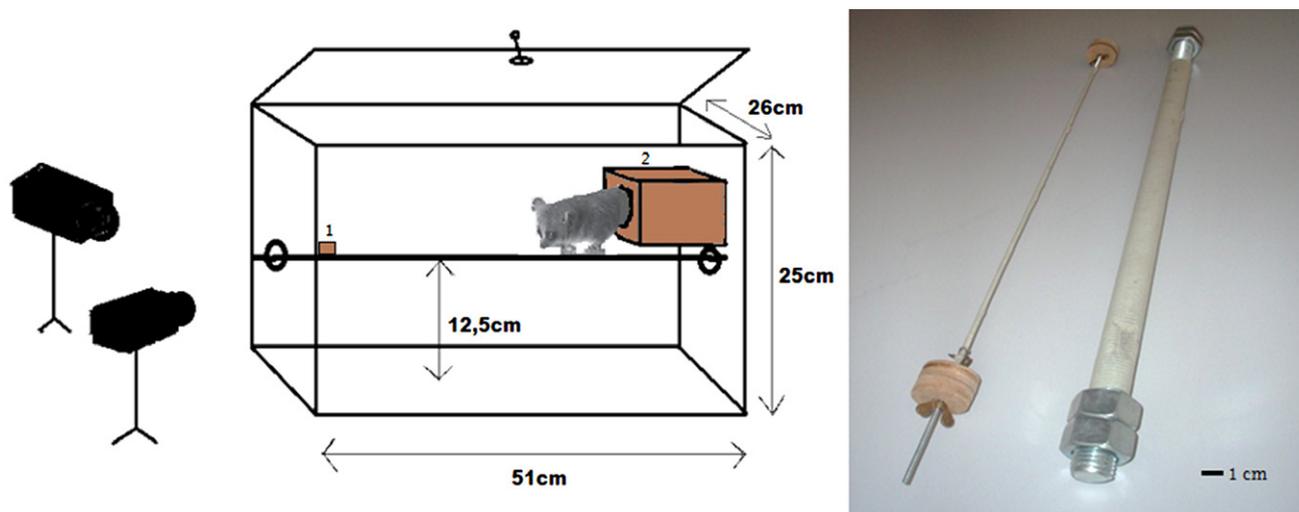


Figure 1 Experimental set-up (left): 1 = food placement; 2 = nest box. And the two substrates used (right): diameters of 2 mm and 20 mm.

We selected three food types on the basis of the mobility of the food: a static fruit, a slow-moving mealworm and a fast-moving cricket. The static fruit consisted of a piece of banana with a volume of *c.* 1 cm³, corresponding roughly to the surface area of the hand of the mouse lemur. The slow-moving food consisted of a crawling mealworm with a size in between 1 and 1.5 cm in length. These prey move very slowly on both substrates. The fast-moving food consisted of crickets between 1 and 1.5 cm in length. These prey moved rapidly across both substrate types.

Procedure

Before recordings, a 2-day habituation in the experimental enclosure was implemented for each individual. The daily recording sessions started at the beginning of the activity period in low light levels, with the experimental set-up lit by a dim red light (20 mW cm⁻¹, equivalent to 0.002 lx). During the first hour or the first 2 h of the dark cycle (2:00 PM to 3:00 or 4:00 PM), individuals were the most active.

For each session, one piece of banana, one mealworm or one cricket was placed on the substrate inside the enclosure. The mealworm and the cricket placed on the substrate moved freely but the banana was pinned onto the substrate. The session started as soon as the food was placed on the substrate, and finished when the individual grasped the food. The individuals were always in their nest box within the enclosure when the food was placed on the substrate and returned to their nest boxes after grasping or after having eaten the food. We collected 10 grasps per type of food for each substrate and for each individual ($n = 60$ grasps per individual). However, one individual (#5) refused to eat crickets. A total of 280 grasps were thus recorded and analyzed. Each individual needed 3–5 days to execute all the grasps.

All data were obtained in unconstrained conditions meaning that the individual was totally free to move out to the nest in order to climb on the substrate and to grasp the food. The individuals were not trained in this task prior the experimental trials.

Data analysis and grasping strategies

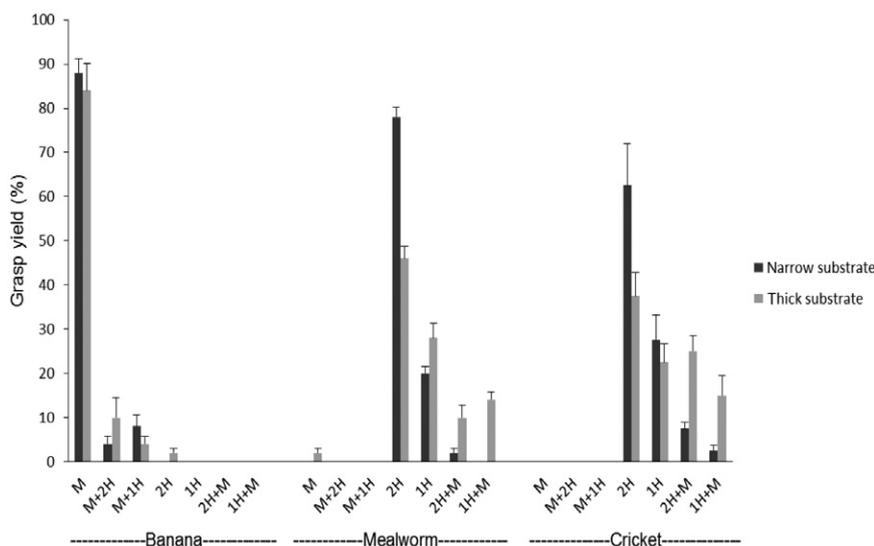
The different grasping strategies were quantified after frame-by-frame analyses of the video recordings. We observed seven grasping strategies: mouth grasp (M), hand-only grasp (1H), bimanual grasp (2H), mouth first followed almost instantaneously by one hand (M + 1H), hand first followed almost instantaneously by mouth (1H + M), mouth first followed almost instantaneously by both hands (M + 2H) and both hands first followed almost instantaneously by the mouth (2H + M).

Statistical analysis

We tested the effect of food properties on grasping strategies using a Friedman one-way ANOVA test for repeated measures based on the data for each individual separately, as well as the data for all individuals combined. Moreover, we tested the effect of substrate for each food type using Wilcoxon matched pairs tests. This allows us to compare the use of the hands or mouth for the two substrates using data at both the individual and the group level. All analyses were performed using the R graphical and statistical software v.3.0.0 (R Development Core Team, Auckland, New Zealand). Some results are presented with their standard error (SEM) and the percentages are presented with the standard deviation (SD). The significance threshold, for the Friedman tests, was set at $\alpha = 0.05$ and all results were Bonferroni corrected. Significance is indicated in the results using the following notation: * $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$.

Table 1 Statistical tests of the effect of substrate diameter on grasping strategy for each individual, for each food (Wilcoxon tests after Bonferroni's correction)

Individual	Static food (banana)	Semi-mobile food (mealworms)	Mobile food (crickets)
1	V = 0, P = NA	V = 2.5, P = 0.02*	V = 14.5, P = 0.5
2	V = 14, P = 0.1	V = 20, P = 0.06	V = 41, P = 0.03*
3	V = 0, P = NA	V = 21, P = 0.7	V = 13.5, P = 0.6
4	V = 1, P = 0.1	V = 10.5, P = 1	V = 48, P = 0.04*
5	V = 0, P = NA	V = 18.5, P = 0.1	–

* $P < 0.05$.**Figure 2** Frequency of grasping strategies used according to food properties and substrate diameters for the whole group. M, mouth grasp; H, unimanual grasp; 2H, bimanual grasp; M + 1H, mouth and one hand grasp; 1H + M, one hand and mouth grasp; M + 2H, mouth and bimanual grasp; 2H + M, bimanual and mouth grasp.

Results

Effect of the substrate diameter on the grasping strategies

For all individuals combined, substrate diameter had a significant effect on grasping strategy when grasping mobile food items (mealworm and cricket), but not when grasping static foods (Wilcoxon matched pairs: banana: $V = 23.5$, $P = 0.72$; mealworm: $V = 505.5$, $P = 0.0014$; cricket: $V = 368$, $P = 0.018$; Table 1). Although the effect of substrate diameter was not significant after Bonferroni correction at the individual level, the frequency of the use of the mouth combined with one or both hands increased on the wide substrate for mobile prey (Fig. 2). However, the proportion of mouth grasping remained similar for static food on both substrates ($88 \pm 3\%$ on the narrow substrate, $84 \pm 6\%$ on the wide one; mean \pm SD). Secondly, more variability in grasp types was observed on the wide substrate than on the narrow one (Fig. 2). Indeed, the individuals on the wide substrate exhibited one additional type of grasp for banana (2H) and two additional types of grasping for mealworms (M, 1H + M). In addition, the bimanual grasp without the mouth (2H) was widely used for catching prey on the narrow substrate ($78 \pm 2\%$ for mealworm; $62 \pm 9\%$ for cricket; mean \pm SD) but less so on the wide

substrate ($46 \pm 3\%$ for mealworm; $37 \pm 5\%$ for cricket; mean \pm SD). Thus, no single one strategy was preferred (all $< 50\%$) for prey capture on the wide substrate (Fig. 2).

We also observed inter-individual differences in grasping strategies. For crickets, individual 4 preferentially used both hands to catch prey on the narrow substrate, and a combination of one or both hands with the mouth on the wide substrate. Similarly, for mealworm capture, individual 5 typically grasped mealworms with both hands on the narrow substrate, but added the mouth on the wide substrate. For banana, a different trend occurred with the individual 2 using the mouth to grasp the fruit on narrow substrate, but using one or both hands in addition to the mouth on the wide substrate, while other individuals used the mouth only.

Effect of food properties on the grasping strategies

A significant effect of food properties on grasping strategy was observed for both substrates when testing all individuals combined (narrow substrate: Friedman chi-squared = 33.38, d.f. = 2, $P < 0.0005$; wide substrate: Friedman chi-squared = 35.64, d.f. = 2, $P < 0.0005$). When testing each individual (Table 2), we noted inter-individual differences. For three individuals, food types had a significant effect on grasping strategy, but for

Table 2 Statistical effect of the food properties on the grasping strategies for each individual on each substrate (Friedman tests)

Individual	Narrow substrate	Wide substrate
1	d.f. = 2, P = 0.00003***	d.f. = 2, P = 0.00009***
2	d.f. = 2, P = 0.3	d.f. = 2, P = 0.86
3	d.f. = 2, P = 0.00004***	d.f. = 2, P = 0.00012***
4	d.f. = 2, P = 0.25	d.f. = 2, P = 0.00023***
5	d.f. = 1, P = 0.00091**	d.f. = 1, P = 0.00091**

** $P < 0.005$.*** $P < 0.0005$.

individual 4, effects of food properties were significant only on the wide substrate, and for the individual 2, no effect of food properties could be demonstrated.

Grasping strategies were characterized by the use of several types of grasps, which differed according to food properties (Table 2, Fig. 2). Four types of grasp (M, M + 2H, M + 1H, 2H) were observed for static food acquisition (banana) where the most commonly used grasp was the mouth (M; more than 80%). Other grasp types were rarely used (less than 10%). Five types of grasp (2H, 1H, 2H + M, 1H + M, M) were observed for mobile prey. The bimanual grasp (2H) without the mouth was preferentially used for mobile foods (more than 35%). Moreover, the hand alone was the second most common type of grasp (more than 20%), followed by hand-mouth combinations (2H + M, 1H + M). The mouth alone was not used except one time by one individual while catching mealworms. Interestingly, when both mouth and hands were both used to grasp food, individuals used more the mouth to initiate the grasping of banana (M + 2H, M + 1H) while using more the hands to grasp mobile prey (2H + M, 1H + M).

Discussion

The aim of this study was to assess whether substrate diameter and food properties influence food-grasping strategies in a small primate, *M. murinus*. As food grasping with the hands is one of the main characteristics of primates, this trait was presumably selected for near the origins of the group. Based on hypotheses of primate origins and on the behaviour of extant species, we predicted that (1) a narrow substrate should increase the use of manual grasping because the feet can more easily close around the substrate, thus enhancing stability and allowing the hands to remain free, and (2) that the presence of moving food should increase the use of manual grasping. The main results supported these two hypotheses, especially at the group level. Results for the effect of the substrate diameter on grasping strategies at the individual level were not significant after correction for multiple testing, probably because of the relatively low sample size.

Nevertheless, a behavioural pattern appeared with different strategies associated with different substrate diameters and food properties, especially for the capture of live prey. Indeed, mouse lemurs modified their strategies and preferentially caught mobile prey with one or both hands, consistent with previous observations in the wild (Petter, 1962; Martin,

1972*a,b*; Charles-Dominique, 1977; Siemers *et al.*, 2007). The preferred use of one or both hands without the mouth for capturing mobile prey appears common to mouse lemurs and other primates including platyrrhines (callitrichids, capuchins), strepsirrhines (galagids, cheirogaleids, lorises), tarsiers and non-primate species such as rats and opossums (strepsirrhines: Petter, 1962; Martin, 1972*a,b*; Charles-Dominique, 1977; Nekaris, 2005; tarsiers: Niemitz, 1984; platyrrhines: Singer & Schwibbe, 1998; Pouydebat *et al.*, unpublished data; rats and opossums: Ivanco *et al.*, 1996). Moreover, the use of the hands was common on the narrow substrate, whereas the mouth was rarely used. In contrast, the use of the mouth combined with the hands increased while grasping prey on the wide substrate. In a previous study, the mouth-hand combination was the most commonly used by *M. murinus* for catching mealworms in a food bowl (mouth-hand combination: 69%), followed by the use of mouth alone (28.1% SD; Scheumann *et al.*, 2011). Thus, the wide substrate seems to favor the use of the mouth for prey capture.

The modification of grasping strategies according to substrate may be related with the habitual environment of *M. murinus*. Indeed, the mouse lemurs possess a powerful pedal grasp with a divergent hallux particularly adapted to grasp small branches improving security and stability (Martin, 1972*a*; Cartmill, 1974*a,b*; Sargis *et al.*, 2007). Considering that the feet of the mouse lemurs are able to grasp and encircle the narrow substrate but not the wide substrate used in the present study, we suggest that the stability of mouse lemurs is enhanced on the narrow substrate allowing them to free their hands for food grasping. This idea is supported by other studies showing that the elongation of digits relative to the palm or sole enables arboreal species to encircle thin substrates, thus enhancing an animal's stability during grasping (Lemelin, 1999; Lemelin & Schmitt, 2007).

Our data suggest that mouse lemurs use two main strategies to catch mobile prey: bimanual and unimanual grasping. The bimanual grasp is widespread within mammals and is used by carnivores (e.g. raccoons: Iwaniuk & Whishaw, 1999), marsupials (e.g. tree kangaroos: Iwaniuk *et al.*, 1998; opossums: Lemelin, 1999), rodents (Whishaw *et al.*, 1998) and tree shrews (Sargis, 2001) suggesting that it is a plesiomorphic feature for primates. The single-handed grasping strategy is rarer among mammals, having been observed in primates (e.g. Lemelin, 1999; Nekaris, 2005; Pellis & Pellis, 2012), some rodents (Whishaw *et al.*, 1998), opossums (Ivanco *et al.*, 1996; Lemelin, 1999), tree shrews (Sargis, 2001) and tree kangaroos (Iwaniuk *et al.*, 1998). Our findings suggest that the capture of mobile food induces the use of a single hand in an arboreal context, likely facilitated by prehensile feet. This is supported by data for other species. For example, Ivanco *et al.* (1996) compared rats and opossums during the grasping of crickets and showed that the arboreal opossums preferred to use a single hand, contrary to rats, which preferred the mouth rather than the hands. Unfortunately, quantified observations of grasping behaviour on arboreal substrates are missing for other species. Finally, sensory guidance could potentially help explain why the capture of mobile prey with the hands is more

efficient than mouth-based capture in primates, but not in arboreal mammals in general. Rodents like the eastern grey squirrel, for example, use their moveable whiskers for guiding the mouth (Hires, Efros & Svoboda, 2013). Primates, in contrast, use their stereoscopic vision to guide their hands during prey capture (Cartmill, 1972).

Concerning the grasping of static foods (banana), the main type of grasp used was the mouth alone, regardless of the substrate. The use of both mouth and hands, or hands alone, was always less common. This is consistent with previous studies on the grasping of small-sized fruit items (Ward & Hopkins, 1993; Reghem *et al.*, 2011; Scheumann *et al.*, 2011). Moreover, grasping static foods with the mouth as observed here for mouse lemurs is commonly observed for other species, yet always on non-arboreal substrates (strepsirhines: Pollock, 1977; Ward & Hopkins, 1993; platyrrhines: Singer & Schwibbe, 1998; non-primate species as rodents: Whishaw *et al.*, 1998; opossums: Ivanco *et al.*, 1996 and tupaia: Joly, Scheumann & Zimmermann, 2012). As is the case for prey grasping, quantitative data do, however, not exist for arboreal substrates.

In summary, the use of the hand in food grasping differed for static and mobile food items (both slow and fast moving) and between substrate diameters. Both the narrow substrate and the moving food increased the use of the hand in food grasping and the data suggest that prey capture associated with the use of narrow branches may have been an important selective pressure driving the evolution of prehensile capacities in the first primates. These results are consistent with the hypotheses on primate origins, which propose that adaptations to both a narrow branch environment as well as visually directed prey capture with hands may be important (Cartmill, 1972, 1974*a,b*; Rasmussen, 1990; Godinot, 2007). However, for both the mouse lemur as well as for other species, the grasping of mobile prey involves the use of the hand independent of substrate diameter (narrow and wide), suggesting that the narrow branch niche is not the only selective factor. Recent studies with small arboreal mammals confirm this suggestion. Indeed, Orkin & Pontzer (2011) showed that eastern grey squirrels (*Sciurus carolinensis*) fed and foraged in terminal branches, yet without developing the features characterizing the morphology of the hands and feet of primates. The results obtained for the European red squirrel further support this hypothesis (Samaras & Youlatos, 2010). Despite a similar lifestyle (i.e. the use of the narrow branches milieu), some mammals thus do not develop the typical morphological characteristics of the hand and foot found among primates. This suggests that these morphological characteristics are not solely the result of the use of the narrow branch niche, but that other factors such as the use of the hand in predation may have played an important role. Thus, we suggest that narrow branch use and insectivory could have provided the ecological conditions needed for the origin of grasping in early primates. The hypothesis that essentially considers the narrow branch niche in association to grasping fruits and flowers (Sussman, 1991) seems insufficient to explain the origins of primate hand. On the contrary, the hypotheses considering the influence of insect predation specialization in the context of moving on narrow

branches (Cartmill, 1972, 1974*a,b*; Godinot, 1991, 2007; Rasmussen, 1990; Kirk *et al.*, 2003) seem more in accordance with our results. To conclude, our results do not refute existing hypotheses on primate origins but rather emphasize predation as a potentially important factor in the elaboration of manual ability and the use of the hands in food grasping in the first primates.

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