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Tails in Action: Comparative Use of the Prehensile Tail and Substrate in *Alouatta macconnelli*, *Sapajus apella*, and *Potos flavus*

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ABSTRACT

Arboreal habitats are three-dimensionally complex and are composed of substrates that differ in size, compliance, and continuity. In response, arboreal vertebrates have evolved morphological and behavioral traits allowing them to successfully move through these environments. Prehensile tails constitute one of such adaptations, yet remain poorly studied. Variation in prehensile tail use between species might result in anatomical variations, as has been shown in primates but remains undocumented in most species. The present study, therefore, sought to describe prehensile tail use and substrate type utilization between two primates, the Guianan red howler (*Alouatta macconnelli*) and Brown capuchin (*Sapajus apella*) and one carnivoran, the Kinkajou (*Potos flavus*). To do so, we used 1431 photographs obtained from camera traps placed in the canopy in French Guyana. The results showed that *P. flavus* exhibits a greater diversity of overall positional and prehensile tail-associated behaviors compared to *S. apella* and *A. macconnelli*. Moreover, *P. flavus* used its tail for both stability and mass-bearing purposes during locomotor and postural behaviors, while *A. macconnelli* and *S. apella* used their tails mainly for mass bearing and stability, respectively, and this was only during postural behaviors. *P. flavus* mostly used large substrates but *A. macconnelli* used more small substrates. *S. apella* showed a preference for both medium and large substrates. Multivariate analyses showed that the three species were well discriminated regarding positional behaviors, with *P. flavus* exhibiting several postural and especially locomotor behaviors not shared by the two primate species, as well as a combination of behaviors shared with either of the two aforementioned species. *A. macconnelli* was mainly characterized by suspensory posture and vertical displacements, whereas *S. apella* mainly used above-branch postures using its tail to anchor itself.

1 | Introduction

In natural ecosystems, the habitat and niche occupied by different species tend to influence the evolution of morphological and behavioral responses, hence, allowing for resource utilization at different spatial-temporal scales. The arboreal environment poses specific challenges for locomotion, mainly due to the limited, discontinuous nature of tree branches as well as their variability in size, compliance, and orientation (Cartmill 1985). Arboreal species possess several distinctive structural adaptations such as limb elongation or reduction, appendages specialized for grasping or clinging and special

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Summary

- Quantitative estimation of positional and tail-associated behaviors in three species using camera traps.
- Important interspecific variations in prehensile tail use.
- Carnivoran species demonstrate more complex locomotor behaviors than the primates.

locomotor modes which allow them to minimize the risk of falling and to move efficiently within the vertical strata of forests (Dublin 1903; Cartmill 1985; Preuschoft 2002; Young 2023). Among such adaptations, grasping limbs have been demonstrated to be functionally relevant for climbing and negotiating fine branches (Cartmill 1974, 1985; Preuschoft 2002; Nyakatura 2019; Young 2023). Another grasping extremity has been considered an adaptation to the arboreal environment, namely the presence of a prehensile tail (Emmons and Gentry 1983). Tails are diverse and play a broad array of ecological and behavioral roles in mammals (Hickman 1979).

Among these, prehensile tails are among the most intriguing, yet least studied (Youlatos 2003; Maniakas and Youlatos 2019). Emmons and Gentry (1983) defined a prehensile tail as "...one which can support alone the weight of the suspended body" even though this definition has been debated as this prerequisite has been considered to drift too far from the initial definition of prehensility (i.e., the capacity of grasping objects; Meldrum 1998). Furthermore, several observations have supported the use of the tail in a somewhat prehensile manner in several species classically not considered prehensile. In primates, behaviors implying coiling of the tail around substrate to support at least some part of the body-weight as well as its use to catch small objects in captive individuals have been reported in Old World primates not considered as prehensile (Dunbar and Badam 2000; Grand 1972; Meldrum 1998). Furthermore, some of those species have been investigated morphologically and grouped with the non-prehensile primates rather than with the prehensile ones (Ankel 1962; Lemelin 1995). Our current knowledge indicates that species using their tails for grasping in a substantial manner have evolved in at least 15 families and 40 genera of mammals (Bezanson 2012), including diprotodont marsupials, didelphid marsupials, pangolins, xenarthrans, carnivorans, primates, and rodents, thus, representing an excellent example of convergent evolution (Youlatos 2003).

Prehensile tails tend to show distinct differences from non-prehensile tails at different anatomical levels. Previous investigations have shown significant osteological, myological, and histological differences between prehensile and non-prehensile tails, especially in primates (Dor 1937; Ankel 1962; German 1982; Lemelin 1995; Organ et al. 2009; Organ 2010; Deane et al. 2014) and carnivorans (Dor 1937; Youlatos 2003; Organ et al. 2009). These studies have notably demonstrated convergence in the shape of the caudal vertebrae associated with an increase of the vertebral body robusticity and an increase in muscle insertion sites, an increase in tail muscle mass, especially in the flexor musculature, a tendinous organization allowing for finer control of individual vertebral segments and the presence of mechanoreceptors in the tip of the tail of some species allowing sensory capacities comparable to those of the hands and feet.

Behavioral studies have explored behavioral differences associated with the use of prehensile tails both between and within taxa. For example, a study on a prehensile-tailed non-primate, *Caluromys philander*, revealed that not only is the prehensile tail crucial during locomotion in preventing falls by serving as an additional grasping limb, but also for carrying leaves used in nest building (Dalloz et al. 2012). Moreover, a comparative ontogenetic study by Bezanson (2012) also showed significantly more frequent use of prehensile tails in juveniles of *Cebus capucinus* and *Alouatta palliata* during foraging and feeding compared to adult individuals. Bezanson (2012) further emphasized the importance of the prehensile tail in mass bearing and its importance in allowing species to exploit other food resources. Similarly, several other studies have described the complexities of prehensile tails in the context of locomotor and postural behaviors (see Fontaine 1990; Turnquist et al. 1999; Youlatos 2002; Schmitt et al. 2005; Mangalam et al. 2022), resulting in a solid body of literature focusing on the association between postural and locomotor (i.e., positional) behaviors and prehensile tail use. However, many of such studies explicitly focused on primate taxa with little emphasis on other mammalian groups possessing similar traits. Furthermore, even if not tested, it has been suggested that tails likely play distinct behavioral roles in other prehensile-tailed species (Meldrum 1998). Consequently, it is important to establish a clear and comparative understanding of whether prehensile-tailed primates and non-primates (especially sympatric species) may employ similar tail-associated positional behaviors. Such information is crucial to understanding why non-related sympatric species seemingly evolve similar adaptive features and how such adaptations may promote survival and possibly niche segregation. To help bridge this knowledge gap, this study sought to describe the use of prehensile tails during positional behaviors as well as substrate type utilization in two primates, the Guianan red howler (*Alouatta macconnelli*) and the Brown capuchin (*Sapajus apella*) and a carnivoran, the Kinkajou (*Potos flavus*), hereafter referred as *A. macconnelli*, *S. apella*, and *P. flavus*, living syntopically in the rain forests of the Guiana Shield.

Overall this study aims at describing the diversity of tail-associated positional behaviors exhibited by the carnivoran *P. flavus* by means of a comparative quantitative framework including two primate species (*S. apella* and *A. macconnelli*). As an important body of literature has already described the positional behaviors of the aforementioned primates through direct observations, their inclusion is also interesting to test the efficacy of camera traps to describe and quantify said behaviors. Data regarding the behaviors of *P. flavus* are critically lacking, implying the use of the tail in a prehensile manner. In this context, one of the main questions this study aims to answer is if *P. flavus* is using its tail like any better-known prehensile primate or if this species exhibits tail-use that is unique compared to any other previously studied species. In primates, anatomical variations have been associated with differences in tail-use between prehensile species (Dor 1937; Ankel 1962; German 1982; Lemelin 1995; Organ 2007, 2010; Deane et al. 2014). Similarities between *P. flavus* and atelids have been highlighted, contrasting with prehensile-tailed cebids, especially regarding anatomical proxies of tail suspension (Youlatos 2003; Organ 2007;

Organ et al. 2009), and thus we might expect more similarities in the positional repertoires of *P. flavus* and *A. macconnelli* compared to *S. apella*. Lastly, primates have often been considered as presenting more diverse positional behaviors than other arboreal mammals (Vilensky and Larson 1989; Cant 1992; Blanchard and Crompton 2011; Fleagle 2013; Schmitt et al. 2016). This study provides data to test if this hypothesis holds true in the case of *P. flavus* and with regard to tail-associated behaviors.

2 | Methods

2.1 | Ethical Statement

Ethical review and approval was not required for the study because animals were not captured or manipulated. This study adhered with the legal requirements applying in French Guiana (France). The research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-human Primates.

2.2 | Study Area

The study was conducted in the mature rainforest of the "Nationale 2" road extending from Cayenne to Saint-Georges (near the Oyapock River), which makes up the border between Brazil and French Guiana (coordinates N3° 55.994′ W51° 50.760′–N4° 02.006′ W51° 59.416′; Figure 1). The study site is composed of a mosaic of mixed forest types where most tree species belong to the Fabaceae, Sapotaceae, Chrysobalanaceae, Burseraceae, and Lecythidaceae families (Coutant et al. 2022).

2.3 | Camera Trapping Protocols and Data Collection

A network of 34 (21 HC600 Hyperfire, 8 Hyperfire2, and 5 XR6 Ultrafire, all from the brand Reconyx) camera traps equipped with infrared motion sensors were installed within the crowns of 11 trees (mostly *Virola kwatae* and *Virola michelii* and only one in a fruiting Sapotaceae tree) ranging from 30 to 40 m high used by frugivorous mammals for an average duration of 50 days. The first period of activity of the camera traps took place from January 30, 2019, to March 18, 2019, plus one camera trap active until May 02, 2019, the second period took place from November 26, 2019, until January 29, 2020, and the third period from January 14, 2022, to March 27, 2022. In each tree, camera traps were set on the trunk, and within the main branches for maximum coverage, with each trap configured to take five photographs when movement was detected. Camera traps were further configured to retake pictures for up to 120 min when animals remained within focal range (see detailed protocol description in Coutant et al. 2022 and Séguigne et al. 2022). Data used in this study only included photos within which focal species were observed. We defined a single observational event (period of positional behaviors) as a group of at least three consecutive photos where positional behavior was observed. At the same time, consecutive photos separated by a minimum of 5 s were considered as independent observational events since the 5 s independence interval was the required time interval without activity for a camera trap to stop picturing. To accurately describe overall and tail-associated positional behaviors, only pictures capturing complete bodies of focal species were considered and classified as either locomotor or postural behaviors following behavioral descriptions from Hunt et al. (1996) (Table S1). Special attention was given to the use of the prehensile tail during each observed positional behavior to infer the potential role or importance of the tail in said behaviors. For the purpose of this study, prehensile tail-associated positional behaviors were defined as locomotor and postural behaviors during which tails fully or partially supported body weight. Thus, positional behaviors observed during which the tail was either fully or partially coiled around the substrate were considered as prehensile tail-associated positional behaviors. For observational events where multiple activities and positional behaviors were observed, we recorded each as a separate activity and positional behavior within the same observational event. Substrate size was

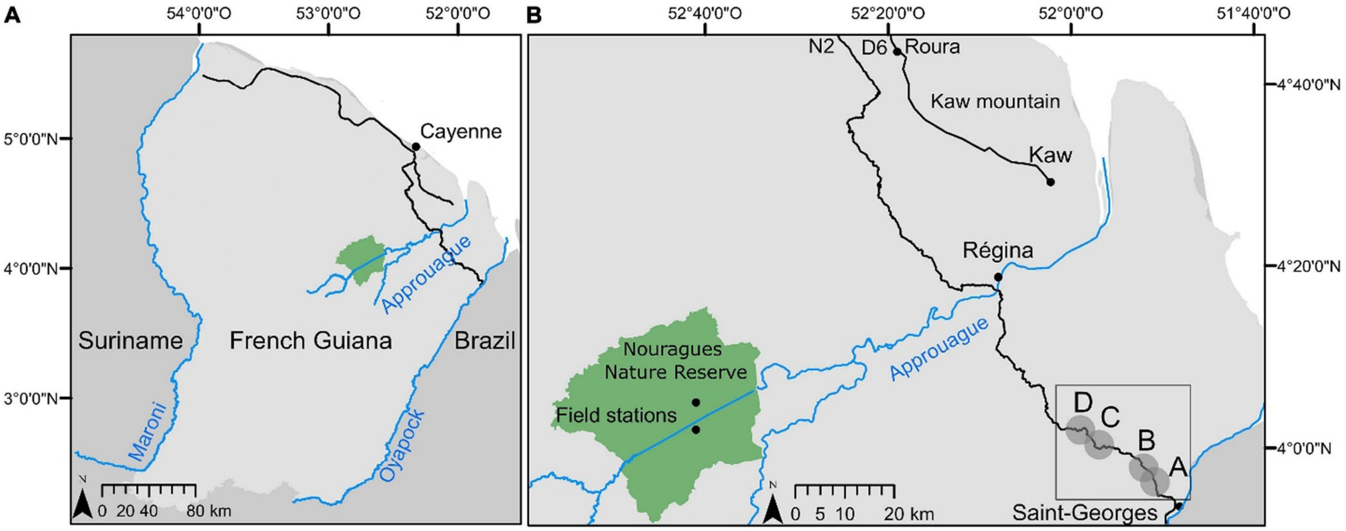

FIGURE 1 | Map of the study area showing camera trap clusters (A, B, C, and D) and their respective locations (Adapted from Coutant et al. 2022).

estimated using the palm grasping coverage of the focal species relative to the branch and categorized as either small (branches that can be fully grasped), medium (branches with half of the substrate covered by the palm), or large (branches with considerably less than half of the substrate covered by the palm of the hand).

2.4 | Data Analysis

Following Granatosky (2018), the Shannon Weiner's diversity index (*H*) was used as a singular measure to estimate the diversity of overall and tail-associated positional behaviors. Positional behaviors were quantified using a descriptive statistical approach such that the frequency was calculated as the number of observational events in which a particular behavior was observed divided by the total number of observational events expressed as a percentage (Table S2). To investigate the overall proportion of tail-associated positional behaviors (i.e., behaviors involving either complete or incomplete tail wrap) in the three focal species, all positional behaviors were split between the ones where the tail was used and the ones where it was not. Total frequencies (in percentages) of these two categories were calculated for each species for the sum of all positional behaviors as well as separately for postural and locomotor behaviors and represented in the form of a barplot. A chi-square test was used to compare the frequency of substrate use within (i.e., between substrate per species) and between species (i.e., between species per substrate).

Multivariate analyses were performed to summarize and provide a graphical representation of the relationship between the species and the frequency of positional behaviors using a data set composed of only the 22 positional behaviors implying the use of the tail in a prehensile manner (Table 2).

First, a principal component analysis (PCA) was realized with the three species as individuals and the frequencies of the 22 behaviors as quantitative variables (Thioulouse et al. 2018; Greenacre et al. 2022). However, when a behavior was observed in a single species only, the observed frequencies for the respective behavior with respect to the other species were computed as zero. However, as PCA calculations rely on Euclidean distances, this analysis is sensitive to zeros (Legendre and Legendre 2012). Furthermore, PCA analyses are known to be more adequate for variables with linear distribution (Legendre and Legendre 2012; Thioulouse et al. 2018), whereas, for the behaviors exhibited by only one species, the distribution will be unimodal.

For those reasons, Correspondence Analyses (CA), which is an ordination method similar to PCA, has been widely used in fields like community ecology to treat data such as frequencies of occurrence of species per site (Greenacre et al. 2022). Indeed, CA, relying on Chi-square distances, has been shown to be less affected by an important number of zeros in data sets and has been suggested to be better suited for unimodal distributions of variables (Legendre and Legendre 2012; Thioulouse et al. 2018). Thus, a CA was performed as well. Following Greenacre (1993), the choice has been made to represent the results of the CA through an asymmetric biplot as it provides a better way to interpret the relative positions between the species variables and the behavior variables. The symmetric biplot can be found in the supplementary materials of this article (Figure S3).

CA has been criticized in community ecology because in studies interested in the abundance of species per site it has been shown that rare species tend to contribute disproportionately to the analysis (Faith et al. 1987). In our case, it means that rare behaviors (i.e., exhibited by only one species) might have the same effect on our analysis. To compensate for this issue Legendre and Gallagher (2001) have proposed a transformation called the Hellinger Transformation following Rao (1995). This transformation is applied to the raw data, followed by a PCA realized on the transformed data. Alternatively, a PCA on variables representing only the shared behavior (i.e., shared by at least two species) was done. These analyses are presented in the supplementary materials (Figures S1 and S2).

Variables regarding the size of the substrate used by the tail (i.e., small, medium, and large), regardless of the positional behavior exhibited were added as supplementary variables (not part of the calculation of the axes but mapped *a posteriori*) in all the aforementioned analyses following Lê et al. (2008).

All analyses were done in R v.4.1.2 (R Core Team 2017), and multivariate analyses were performed using the package FactoMineR (Lê et al. 2008).

3 | Results

We examined 1431 pictures (289 observational events), of which 15.16% ($N = 42$ observational events), 37.87% ($N = 119$), and 46.96% ($N = 128$) showed positional behaviors from *A. macconnelli*, *S. apella*, and *P. flavus*, respectively. Among those observational events, 63 positional behaviors were recorded for *A. macconnelli* (including 21 locomotor behaviors and 42 postural behaviors), 201 for *S. apella* (including 82 locomotor behaviors and 119 postural behaviors), and 240 for *P. flavus* (including 112 locomotor behaviors and 128 postural behaviors). Regarding the frequency of tail-use in a prehensile manner, *A. macconnelli* exhibited by far the highest frequency at 58.73%, followed by *P. flavus* at 25.83%, and lastly, *S. apella* at 10.45% (Figure 2).

Nevertheless, *P. flavus* showed the most diverse display of overall positional and prehensile tail-associated behaviors compared to *S. apella* and *A. macconnelli* (Table 1). Furthermore, *S. apella* showed a more diverse display of postural behaviors compared to *A. macconnelli*, while the opposite was observed for locomotor behaviors. The tail suspension (59.46%), squatting (23.81%), and full crouch postures (16.13%) were the most dominant tail-associated behaviors observed in *A. macconnelli*, *S. apella*, and *P. flavus*, respectively. Nevertheless, *P. flavus* further employed its prehensile tail in other positional behaviors, including tail suspends postures (12.90%) and tail suspend drops (11.29%), while tripodal postures made up 18.92% of all tail use behaviors from *A. macconnelli* (Table 2). Moreover, *P. flavus* made significantly more use of large substrates during tail grasping behaviors in comparison to other substrate types ($X^2 = 139.63$, $d.f. = 70$, $p = 1.53\text{e}{-06}$) and both

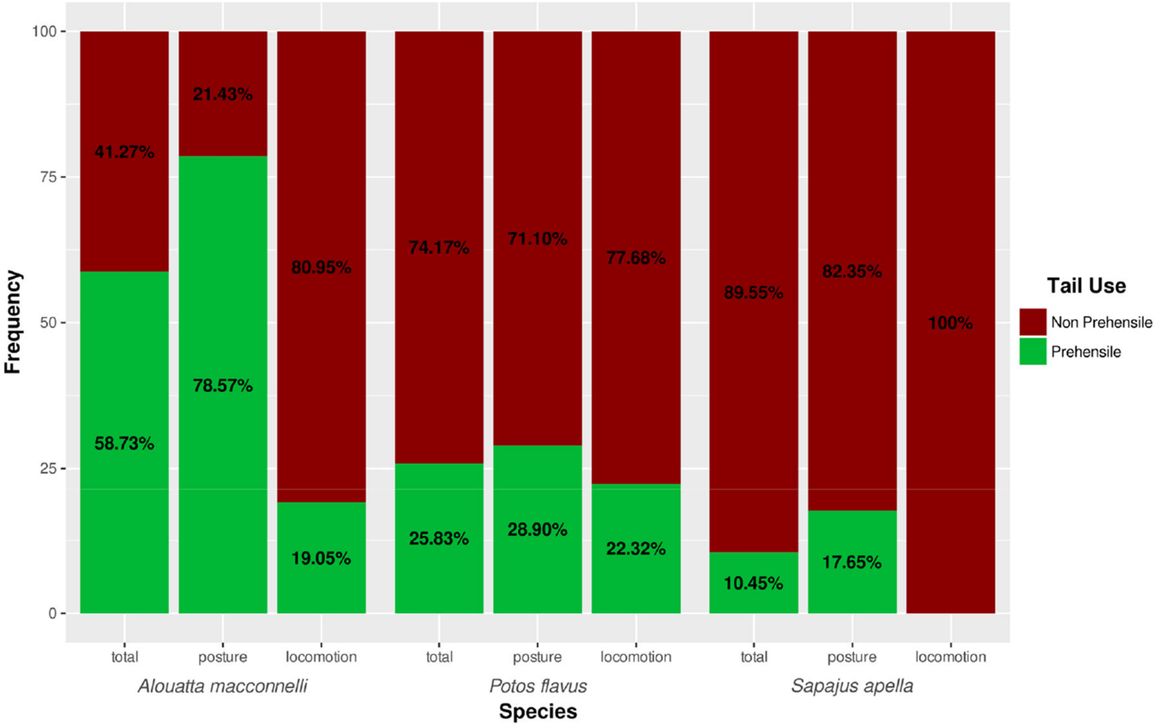

FIGURE 2 | Barplot representing the frequencies (percentages) of positional behaviors in relation to tail use for *Alouatta macconnelli* (left), *P. flavus* (middle), and *Sapajus apella* (right). For each species, the left barplot represents all positional behaviors, the middle one postural behaviors and the right one locomotor behaviors. Green represents the behaviors where the tail is used in a prehensile manner, and brown where it is not.

primates ($X^2 = 130.06$, $d.f. = 2$, $p < 2.20\text{e}{-16}$). *S. apella* used medium substrates significantly more ($X^2 = 27.75$, $d.f. = 2$, $p = 9.42\text{e}{-07}$) than *P. flavus* and *A. macconnelli* while simultaneously showing a significant preference for both medium ($X^2 = 129.41$, $d.f. = 48$, $p = 2.11\text{e}{-09}$) and large substrates ($X^2 = 103.17$, $d.f. = 42$, $p = 4.64\text{e}{-07}$). Interestingly, *A. macconnelli* showed significantly greater use of small substrates ($X^2 = 38.27$, $d.f. = 10$, $p = 4.99\text{e}{-05}$) compared to other substrate types but not when compared with *S. apella* and *P. flavus* ($X^2 = 1.87$, $d.f. = 2$, $p = 0.39$).

Regarding the PCA including all behaviors (Figure 3), the first axis tended to discriminate *P. flavus* from the two primate species and is mainly explained by the behaviors “cautious pronograde bridge,” “cling walk,” “crouched quadrupedal walk,” “hind limb cling,” “inverted quadrupedal walk,” “ladder climb,” “pronograde leap,” “tail hind limb suspend drop,” and “tail suspend drop” as well as “tail hind limb suspend” and “full crouch” to a lesser extent. Overall, this axis is mainly explained by the fact that *P. flavus* tends to exhibit many positional behaviors that are not shared by any of the other species.

The second axis tends to split *S. apella* and *A. macconnelli*. *S. apella* is defined by the behaviors “bipedal stand,” “quadrupedal stand,” “sit,” “squat,” and “tripedal stand,” whereas *A. macconnelli*'s position in the behavioral space is explained by the behaviors “bimanual pull up,” “head first descent,” “supinograde bridge,” “tail suspend,” and “tripodal posture.” *S. apella* seems to be mainly characterized by static behaviors (sitting and standing), while *A. macconnelli* appears to be mainly defined by vertical movements both downward (“tail suspend” and “head first descent”) and upward (“bimanual pull up”). On this axis, *P. flavus* exhibits an intermediate position between *S. apella* and *A. macconnelli*, which can be explained by the fact that it tends to exhibit postural behaviors similar to *S. apella* while being static above branches but at the same time share with *A. macconnelli* the tendency to suspend itself and realize headfirst descent behaviors. Regarding the substrate size, *A. macconnelli* is strongly associated with the use of small substrates. *P. flavus* tends to be characterized by the use of large substrates as well as being strongly negatively associated with the use of medium-sized substrates compared to the two other species.

The Hellinger-transformed PCA (Figure S1) tends to show similar results as the PCA on the non-transformed data. The main differences being that “head first descent,” “supinograde bridge,” “tail hind limb suspend,” and “tail suspend” seems more shared between *A. macconnelli* and *P. flavus* and that “bimanual forelimb crouch,” “bipedal stand,” and “quadrupedal stand” seem more shared between *S. apella* and *P. flavus*.

The PCA presenting only shared behaviors (Figure S2) has a first axis defined by the differences between *S. apella* and *A. macconnelli* and a second one where *P. flavus* is separated from the two primate species.

The first axis of the CA (Figure 4) tends to separate *S. apella* and *A. macconnelli* with *P. flavus* occupying a rather intermediate position although closer to *A. macconnelli*. *S. apella* is associated with the behaviors “bipedal stand,” “quadrupedal stand,” “sit,” “squat,” and “tripedal stand,” and *A. macconnelli* with the behaviors “bimanual pull up,” “head first descent,” “supinograde

TABLE 1 | Scores for the Shannon Weiner's diversity index.

	Overall	Postural	Locomotory	Tail-associated
Potos flavus	2.79	2.10	2.09	2.65
Sapajus apella	2.19	1.89	0.96	1.93
Alouatta macconnelli	2.32	1.62	1.82	1.57

TABLE 2 | Frequency of prehensile tail use during positional behaviors.

	Potos flavus (%)	*Sapajus apella* (%)	*Alouatta macconnelli* (%)
Crouched quadrupedal walk	4.84	0.00	0.00
Inverted quadrupedal walk	3.23	0.00	0.00
Cling walk	1.61	0.00	0.00
Pronograde leap	3.23	0.00	0.00
Ladder climb	3.23	0.00	0.00
Bimanual pull up	0.00	0.00	2.70
Head first descent	1.61	0.00	5.40
Cautious pronograde bridge	6.45	0.00	0.00
Supinograde bridge	1.61	0.00	2.70
Tail-suspend drop	11.29	0.00	0.00
Tail-hind limb suspend drop	3.23	0.00	0.00
Tail-suspend	12.90	0.00	59.46
Tail-hind limb suspend	6.45	0.00	2.70
Quadrupedal stand	6.45	14.28	2.70
Tripedal stand	0.00	14.28	0.00
Bipedal stand	6.45	14.28	0.00
Sit	0.00	14.28	0.00
Squat	0.00	23.81	2.70
Hind limb cling	1.61	0.00	0.00
Tripodal posture	4.84	9.52	18.92
Full crouch	16.13	4.76	0.00
Bimanual forelimb crouch	4.84	4.76	2.70

bridge," "tail suspend," and "tripodal posture." As for the PCA results, *S. apella* tends to use its prehensile tail in static behaviors on large branches, while *A. macconnelli* uses its prehensile tail for vertical upward and downward movements.

On the second axis, *P. flavus* tends to be separated from the two other species. It is associated with the behaviors "cautious pronograde bridge," "cling walk," "crouched quadrupedal walk," "hind limb cling," "inverted quadrupedal walk," "ladder climb," "pronograde leap," "tail hind limb suspend drop," and "tail suspend drop" as well as "tail hind limb suspend" and "full crouch" to a lesser extent. The distribution along this axis can be mainly explained by the fact that *P. flavus* tends to use its prehensile tail in a wide array of positional behaviors that are not shared with the other species.

Lastly, regarding the substrate sizes, *A. macconnelli* is strongly associated with the use of small substrates, whereas *P. flavus* tends to be slightly associated with larger substrate sizes. However, *P. flavus* tends to be strongly negatively associated with medium substrates, whereas the two other species tend to be slightly positively associated with those substrates.

Overall, all the multivariate analyses provide similar results regarding the relationship between the species and the frequencies of positional behaviors.

4 | Discussion

Arboreal habitats are characterized by extreme variations in substrate orientation, compliance, continuity, and diameter. Such complexities are considered very crucial selective pressures impacting the ability of arboreal mammals to efficiently traverse their environment while effectively reducing the risk of injury and metabolic costs (Granatosky 2018). Hence, arboreal species exhibit a plethora of behavioral and morphological adaptations (Cartmill 1985). Climbing encompasses a great

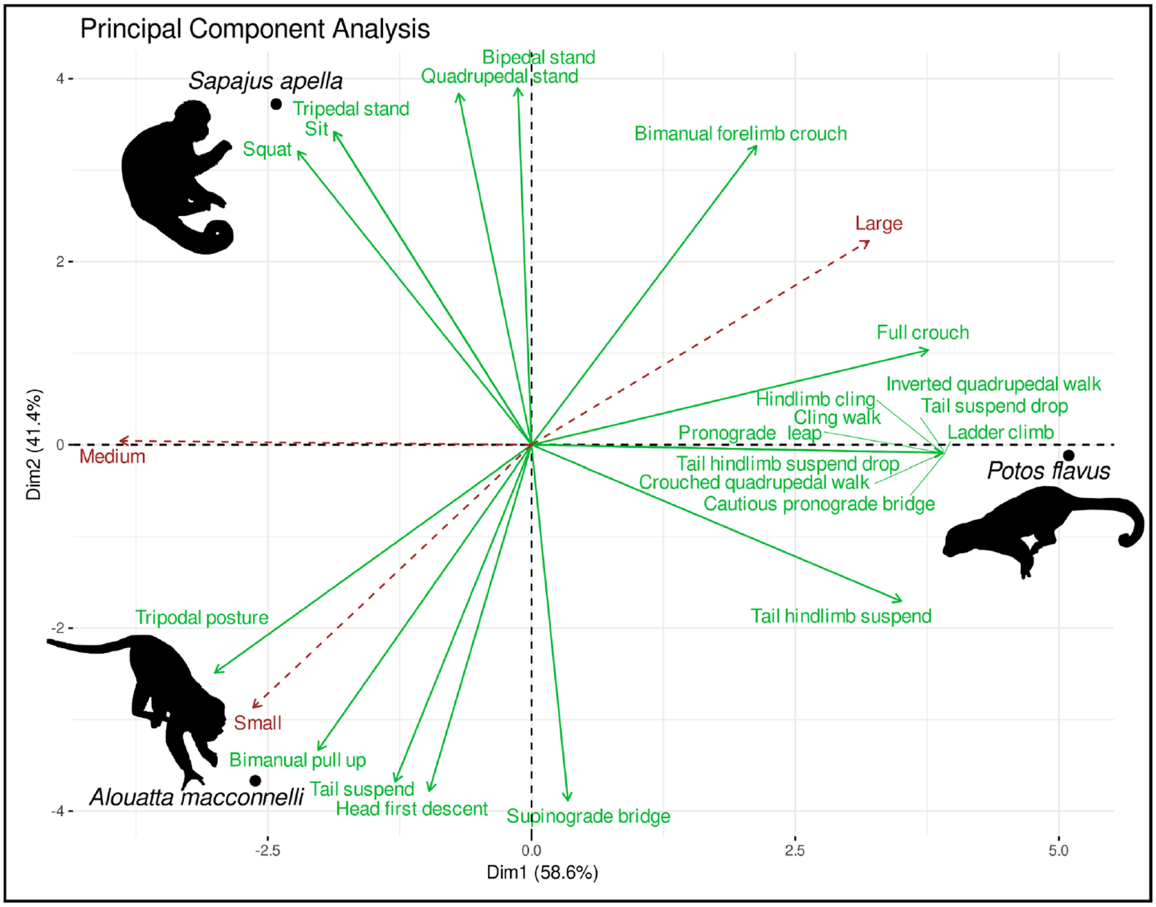

FIGURE 3 | Plot of the principal component analysis, including all behavioral variables. Black points represent the species, green arrows correspond to the positional behaviors, and dashed brown arrows to the supplementary variables, that is, the substrate sizes. The first axis explains 58.6%, and the second axis explains 41.4% of the observed variance.

diversity of locomotor strategies and associated morphological adaptations varying between species and influenced notably by body size and overall morphology (Cartmill 1985; Preuschoft 2002, Young 2023). In this context, prehensile-tailed species appear to be fairly diverse in their ecology, body sizes, overall morphology and general locomotor behaviors (Emmons and Gentry 1983; Meldrum 1998). Thus variation is expected in the way they use their prehensile tails as well, as Meldrum (1998) stated: "It is unlikely, however, that the tail serves identical behavioral roles in all of these taxa." This study complements previous key publications (Fleagle and Mittermeier 1980; Bergeson 1996, 1998; Youlatos and Gasc 2001; Bezanson 2006, 2009, 2012) comparing positional behavior in the wild among arboreal mammals co-occurring and using similar ecological niches, notably in adding for the first time a nocturnal species (i.e., *P. flavus*). Our results demonstrate an important variation between the three studied species regarding their positional behaviors implying tail-use (Figures 5 and S4).

Our data suggest that *A. macconnelli* tends to use its prehensile tail often in vertical movements (headfirst descent, tail suspend, bimanual pull up) and among those a lot of these imply body weight support (headfirst descent, tail hind limb suspend, tail suspend). Suspensory behaviors using only the tail were the most common tail-associated behavior observed for *A. macconnelli* in this study. These results are consistent with previous studies of the positional behavior of different species in the genus *Alouatta*, notably for headfirst descent (Youlatos and Gasc 1994) and especially regarding the importance of tail suspension in postural behaviors (Fleagle and Mittermeier 1980; Cant 1986; Gebo 1992; Bezanson 2009). It is noteworthy that, unlike our results, the tail suspension is rarely described as the main feeding posture even though it is reported to represent a consistent part of the postures realized (e.g., one-third of the observation for Youlatos and Guillot 2015 or 20% in Mendel 1976). Such differences might be explained by differences in the data acquisition method or in the spatial structure of the trees where those observations were made (Bergeson 1998). Another contrasting result is the frequency of quadrupedal walking reported. Our results did not show any use of the tail in a prehensile manner during these behaviors, which is consistent with previous results (Lawler and Stamps 2002). However, it is considered the main locomotor mode exhibited by *Alouatta* (Mendel 1976; Fleagle and Mittermeier 1980; Gebo 1992; Bicca-Marques and Calegaro-Marques 1995; Bergeson 1996). Although in our data, quadrupedal walk was, in fact, the most frequent locomotor mode, it was less common (9.5% of observations) than for *S. apella* (31.3% of observations) or *P. flavus* (20.8% of observations). Results by Bezanson (2006) revealed similar frequencies between *A. palliata* and *C. capucinus* (a close relative of

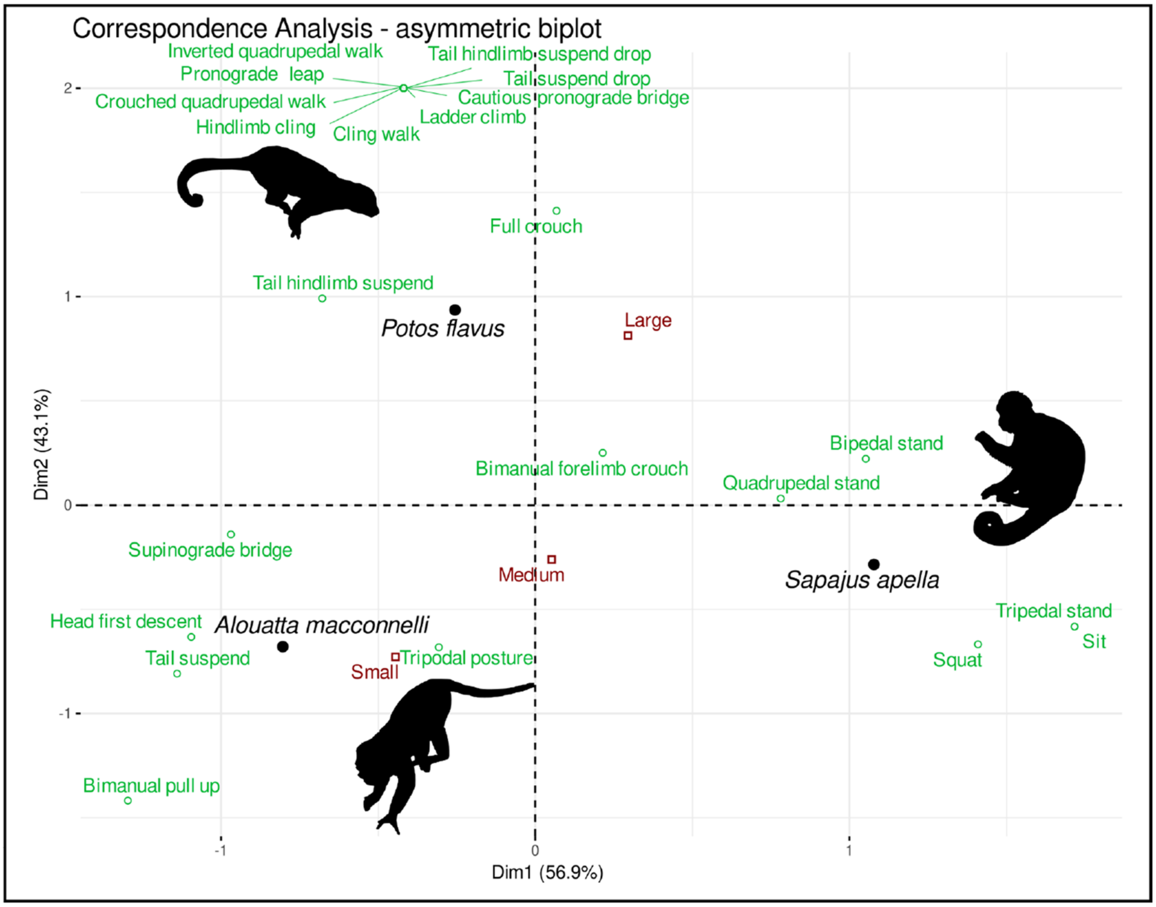

FIGURE 4 | Asymmetric biplot for the Correspondence Analysis representing the "behavior" variables mapped onto the "species" space. Black points represent the species, green circles correspond to the positional behaviors, and brown squares to the supplementary variables, that is, the substrate sizes. The first axis explains 56.9%, and the second axis explains 43.1% of the observed variance.

S. apella previously assigned to the same genus). A possible reason for this relative lack of observation might be the relatively smaller sample size of *A. macconnelli* in our data set (about half the sample size of *P. flavus* and *S. apella*). However, the overall similarity between our other results and the literature tends to support the robustness of our data set. Alternatively, it might be due to differences in the data acquisition methods. Indeed, even if camera traps can provide important advantages compared to direct observation, including the ability to register behaviors continuously for extended periods of time, it presents the disadvantage of a relatively narrow field of view and a fixed angle. Consequently, if quadrupedal walking is used for long-distance travel across trees, there is a possibility that the fixed angles and limited field of view of the camera traps may have missed such behaviors, whereas a direct observer would not. Overall, our results show that in *A. macconnelli*, the prehensile tail is mainly used for postural behaviors in accordance with the literature.

S. apella appears to be using its prehensile tail to engage mostly in above-branch postures where the tail is used to anchor onto the substrate, hence providing increased stability. Our results are in accordance with previous literature on *Cebus*/*Sapajus* positional behaviors. Bezanson (2009) noted that squat and quadrupedal stand were among the most used postural behaviors in *C. capucinus*, and Gebo (1992) mentioned that the frequency of use of a quadrupedal stand was an important difference between *C. capucinus* and *A. palliata*. Furthermore, Garber and Rehg (1999) observed that sitting was the dominant posture while feeding in *C. capucinus*, and so did Youlatos (1999) for *S. apella*, adding that this posture was associated with the use of the tail in a prehensile manner. Our results further confirmed that quadrupedal walk was the main locomotor mode as previously established for *S. apella* (Youlatos 1999; Youlatos and Gasc 2001; Youlatos and Meldrum 2011) and for *C. capucinus* (Garber and Rehg 1999, Bezanson 2009). On the other hand, our observations contrast with the literature regarding tail suspend and tail hind limb suspend behaviors. We did not record any of these behaviors for *S. apella*. However, suspensory behaviors implying tail use have been documented even though described as rare or less frequent than in other prehensile-tailed platyrrhines (Gebo 1992; Bergeson 1998; Garber and Rehg 1999; Youlatos 1999; Bezanson 2009). Still, Garber and Rehg (1999) observed that in total tail suspend and tail hind limb suspends accounted for about 12% of the postural behaviors during feeding and foraging. Furthermore they also described diverse below branch postures as well as locomotor behaviors like tail drops. As those behaviors are associated with feeding and foraging, the distribution of the fruits present in front of the camera traps might explain why such behaviors are lacking in our study. Another possible explanation for these differences might be the interspecific variation in tail-use and

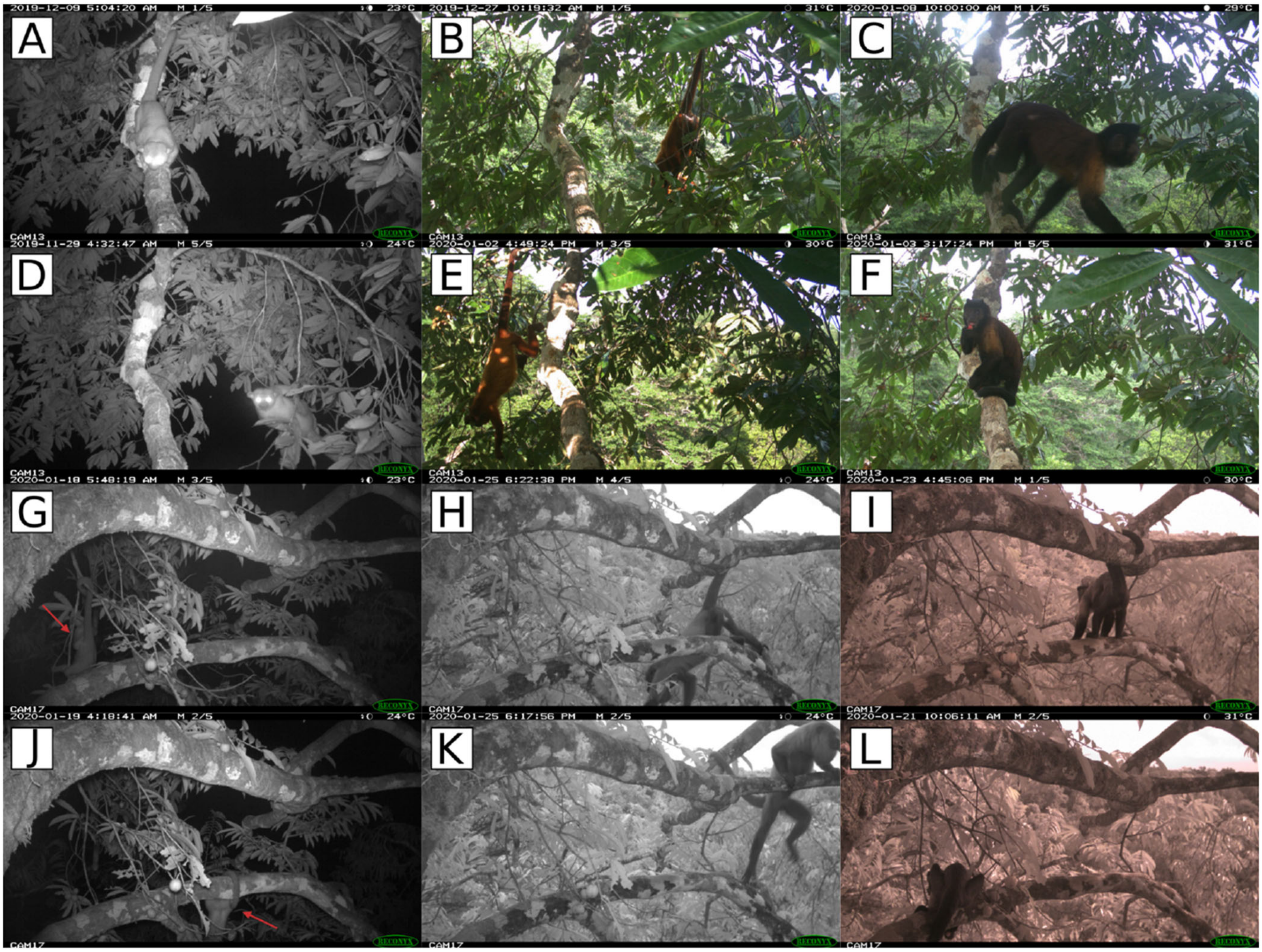

FIGURE 5 | Differences in positional behaviors and associated tail-use for the three species studied. Pictures (A)–(F) correspond to one camera trap (CAM 13), and pictures (G)–(L) correspond to another one (CAM17). Left column depicts positional behaviors of *Potos flavus*, middle column of *Alouatta macconnelli*, and right column of *Sapajus apella*.

positional behaviors among prehensile-tailed cebids. Indeed, the *Cebus* genus recently underwent a division into two genera, *Cebus* on the one hand and *Sapajus* on the other hand, based on molecular, morphological, ecological, and behavioral data (Alfaro et al. 2012). Studies conducted before this split tended to consider the *Cebus* genus as a homogeneous taxonomic unit when discussing variations in behaviors among platyrrhines, even though Garber and Rehg (1999) stated that species among the *Cebus* genus species tend to differ in "size, diet, and modes of habitat exploitation." Regarding the amount of studies available in the literature we did the same to contextualize our results regarding *S. apella*. However, most of the studies reporting tail suspend behaviors were focused on *C. capucinus* (Gebo 1992; Bergeson 1998; Garber and Rehg 1999; Bezanson 2009). Furthermore, Youlatos (1999) compared two species, *Cebus olivaceus* and *Cebus apella* (i.e., *S. apella*), and noted that "Suspensory postures were quite infrequent in *C. apella*, while they represented a considerable proportion in *olivaceus*." However, he argued that this could be the result of the smaller number of observations for *C. olivaceus* compared to *S. apella*. With regard to the existing literature, our results tend to suggest that there might be a real difference in positional behaviors between the genera *Cebus* and *Sapajus*.

The pattern of tail-use mainly for postural behaviors observed in the genus *Alouatta* is often described as contrasting with what is observed in other atelid species that tend to also use their prehensile tails for locomotor behaviors such as tail-assisted brachiation (see Fleagle and Mittermeier 1980; Cant 1986; Youlatos and Gasc 2001). Similar observations regarding the use of the prehensile tail mainly for postural behaviors in *Cebus*/*Sapajus* as well as the tendency to travel using a quadrupedal walk have led some authors to draw parallels between *Cebus*/*Sapajus* and *Alouatta* in comparison to the other prehensile-tailed platyrrhines (Johnson and Shapiro 1998; Garber and Rehg 1999; Youlatos and Meldrum 2011). Despite those similarities, our results suggest important differences in positional behaviors between *A. macconnelli* and *S. apella*. Unlike in *A. macconnelli*, we did not record below branch tail suspend postures for *S. apella*. Rather, we found that *S. apella* utilized their prehensile tail mainly in static postures above horizontal medium to large branches (sit, squat, quadrupedal stand, tripedal stand, bipedal stand).

P. flavus appears to use its tail to engage in a wide array of above- and below-branch postures. Contrary to the two primates, tail-assisted locomotor behaviors are quite frequent in *P.*

flavus, accounting for about 40% of the tail-associated behaviors observed. While tail use for locomotor behavior in *A. macconnelli*, which is second in frequency, accounts for only 8% of the tail-assisted behavior observed. Furthermore, the locomotor behaviors of *P. flavus* appear quite diverse, encompassing above- and below-branch, head up and head down, and vertical and horizontal movements. Interestingly, *P. flavus* tends to share tail-assisted behaviors with both *A. macconnelli* on one hand and *S. apella* on the other hand. Like *S. apella*, it uses its tail for anchoring itself during above-branch postural behaviors (quadrupedal stand, bipedal stand, full crouch). Yet, similar to *A. macconnelli*, *P. flavus* also engaged in suspensory tail-assisted behaviors (tail suspend, tail hind limb suspend) quite regularly (about 19.3% of observed behaviors and 33.8% including tail suspend drops). Studies on the positional behaviors of *P. flavus* are scarce, but McClearn (1992) qualitatively described tail-hind limb suspension for this species. However, to the best of our knowledge, suspension by the tail only has never been described for *P. flavus*. Our results show that it is a rather frequent behavior, being the second most common behavior for this species. Furthermore, our observations suggest that it might be more common than tail hind limb suspend. Tail suspend accounted for 12.9% of observed behaviors and 24.2%, including tail suspend drops, while tail hind limb suspend accounted for 6.4% of observations and 9.6%, including tail suspend drops.

Interestingly, our three species show variation in the way they cross discontinuities in the arboreal environment. Gap-crossing strategies are key components of the locomotor repertoires of climbing species. Cartmill (1985) distinguished two major types of climbing species, the slow climbers on the one hand and the acrobatic climbers on the other hand and described a set of morphological and behavioral adaptations associated with these two strategies. The main difference resides in their gap-bridging strategies, with cautious bridging behaviors for slow climbers and leaping for acrobatic climbers. He further associated slow climbers, and thus, bridging behaviors and prehensile tails, arguing that the loss of the balancing function of the tail resulted either in a tail reduction/loss or in the origin of a prehensile tail. *Alouatta* is particularly known to cautiously bridge across gaps (see Youlatos and Guillot 2015). Although not observed in high frequencies, we noted that *A. macconnelli* crossed discontinuous gaps only by bridging, primarily by using their prehensile tails coupled with hind limbs to hold on to the previous substrate. We observed that *S. apella* dominantly crossed gaps through leaping without using its prehensile tail, which is in accordance with the literature on *Sapajus* (Youlatos 1999) and *Cebus* (Gebo 1992; Bergeson 1996; Garber and Rehg 1999) even though Youlatos (1999) still noted an important role of tail-assisted bridging. Regarding *P. flavus*, McClearn (1992) observed cautious bridging in captive animals but noted discrepancies in previous literature. Indeed, Enders (1935) mentioned bridging when Emmons and Feer (1990) observed leaping from branch to branch. Our results show that *P. flavus* does engage in both gap-bridging quite frequently. Overall, it suggests that some prehensile-tailed species tend to prefer leaping over bridging.

Regarding substrate sizes, our results indicate that even though our three species made use of each size, they demonstrated preferences for particular substrates. *A. macconnelli* demonstrated preferences for small substrates, whereas *P. flavus* used mostly large substrates, and *S. apella* used its tail to grasp medium to large substrates. Regarding *P. flavus*, too few data are available in the literature to contextualize this result, and further studies, especially in other forest types, would be needed to confirm this pattern. *A. macconnelli* has been previously described to use its tails on small branches during suspensory postures while feeding and foraging (Mendel 1976; Bergeson 1998). Still, Bezanson (2012) noted that during feeding and foraging, it used its tail equally on small (35%) and medium (39%) substrates. This study also investigated substrate sizes used by the tail of *C. capucinus* and showed that during feeding and foraging, this species predominantly used small substrates (81%), which contrasts with our results for *S. apella*. Garber and Rehg (1999) found similar results for *C. capucinus* with 68% of small substrates used during feeding and foraging. However, as with the differences in tail suspend behaviors discussed above, it is difficult to know whether this is related to intergeneric differences and highlights the need for further studies on *S. apella*.

Regarding the high frequency of tail use in contexts of feeding and foraging in many species, prehensile tails have been described as playing an important role in acquiring food items otherwise unreachable (Mittermeier and Fleagle 1976; Bicca-Marques and Calegaro-Marques 1993; Youlatos 1993; Youlatos and Guillot 2015). This study illustrates that beyond the overall increase in food accessibility, inter-specific variations in prehensile tail use might be linked to different exploitation strategies of the same resources. Indeed, all three species are generally phytophagous, and even if preferences for different food items have been documented with *Alouatta* being mainly folivorous (Mittermeier and van Roosmalen 1981; Rosenberger 1992; Strier 1992; Bergeson 1998), *Sapajus* demonstrating preferences for hard fruits but also feeding on invertebrates (Mittermeier and van Roosmalen 1981; Rosenberger 1992; Zhang 1994, 1995; Bergeson 1998), and *Potos* eating mainly fruit and nectar (Charles-Dominique et al. 1981; Julien-Laferrière 2006), all three of them include the consistent amount of fruits in their diet (Charles-Dominique et al. 1981; Mittermeier and van Roosmalen 1981; Rosenberger 1992; Bergeson 1998; Julien-Laferrière 2006; Séguigne et al. 2022). Furthermore, in the specific trees where the camera traps were placed (*Virola* spp.), fruit consumption has been demonstrated (Séguigne et al. 2022) for these three species. Séguigne et al. (2022) further showed that these species eat fruits of the same size, suggesting that the species examined here might be competing for the same resources to some extent. However, patterns of temporal activity provided by the camera trap data show that the three species are active at different times (Séguigne et al. 2022). In addition to this temporal segregation, the difference in substrate size used by the tails demonstrates a pattern of spatial partitioning within the tree crown. Indeed, the differences in the sizes of the substrates also reflect the part of the tree crown explored by the species. *A. macconnelli*'s affinity for small substrates is associated with foraging behaviors on the terminal branches, where it tends to adopt suspensory postures to access food items. These results are in accordance with previous studies describing *Alouatta*'s tendency to explore the periphery of the tree crown (Mendel 1976; Bergeson 1996). In contrast, *S. apella* engaged in more above-branch postures while reaching with the forearms to grab food and the tail used to anchor onto the substrate. Such behaviors were mostly performed on the main branches directly emerging from the trunk. *Cebus* is described as less restricted to the crown periphery compared to *Alouatta* and *Ateles* by Bergeson (1996). In addition, Mittermeier and van Roosmalen (1981) noted that in the canopy, *Sapajus* tended to occupy the lower and middle parts, while *Alouatta* tended to occupy the medium and higher parts. Even though terminal branch feeding has been documented in *C. capucinus* (Garber and Rehg 1999) we did not record such behaviors for *S. apella*. In our study, where species co-occur in the same trees to exploit the same resources, these results suggest spatial partitioning between the two species of diurnal primates. These findings are in accordance with previous literature as Fleagle and Mittermeier (1980) stated that "monkeys with similar diets show locomotor and habitat differentiation." The role of differentiated locomotor patterns in niche partitioning has even been considered as one of the plausible explanations for the radiation and current diversity of platyrrhines as a whole (Rosenberger et al. 2009; Youlatos and Meldrum 2011).

Our results also contrast a long-standing statement regarding the complexity of positional behaviors in arboreal mammals and the specificity of primates. Indeed arboreal primates have often been considered to exhibit a higher diversity in their positional behaviors than other climbing mammals (Vilensky and Larson 1989; Cant 1992; Blanchard and Crompton 2011; Fleagle 2013; Schmitt et al. 2016). In the current study, although the focal species displayed a wide range of positional behaviors exclusive to either a single species or shared among species, we found no evidence to support this assumption. On the contrary, our data suggest that *P. flavus* displays greater diversity of both locomotor and postural behaviors than the two primate species. Furthermore, *P. flavus* appeared to be characterized on one hand by behaviors, especially regarding locomotion, that is unique to it, and on the other hand, to share postural and locomotor behaviors with *A. macconnelli* as well as *S. apella*. Both primates tended to present highly contrasting behavioral repertories, notably regarding gap-bridging strategies, the frequencies of suspensory behaviors and above- versus below-branch postures. Thus, *P. flavus* appears like a climbing generalist, whereas the two primates tend to exhibit different positional behaviors associated with distinct foraging strategies. Youlatos and Meldrum (2011) previously stated that positional diversity among platyrrhines was differently distributed between extant species, which is also the pattern observed in our results. Those results tend to contradict the hypothesis regarding the specificity of primates compared to other mammals and are consistent with previous results by Granatosky (2018). The estimations of behavioral diversity shed light on another interesting result. Regarding tail-associated behaviors, *P. flavus* is the species with the highest behavioral diversity, while *A. macconnelli* is the species showing the lowest diversity. However, when looking at the frequency of tail use in a prehensile manner, *A. macconnelli* is using its tail the most (58.73%), followed by *P. flavus* (25.83%) and *S. apella* (10.44%). These results show that the diversity of behaviors and frequency of tail use are not necessarily associated.

Sapajus/*Cebus* tend to be considered semi-prehensile by some authors (Emmons and Gentry 1983; Mangalam et al. 2022). This categorization is based on definitions provided by Emmons and Gentry (1983), stating that "A prehensile tail is one which can support alone the weight of the suspended body; semiprehensile tails can be wrapped around branches and support a significant part, but not all, of the body weight." However, this definition and the relevance of the concept of semi-prehensility have been highly debated, as the prerequisite of suspension by tail only has been considered to drift too far from the initial definition of prehensility (Meldrum 1998). In our study, no tail suspend behaviors were recorded for *S. apella* even though previous studies have demonstrated that such behaviors might occur, especially in *Cebus* (Bergeson 1998; Garber and Rehg 1999; Youlatos 1999 and Bezanson 2009). Furthermore, regarding the frequency of tail-use, *S. apella* appears to be the species using its tail the least in a prehensile manner (10.44%), which is consistent with the literature (Bergeson 1996; Bezanson 2012) and arguing in favor of the semi-prehensility of *S. apella*. However, when behavioral diversity associated with tail-use is considered, *S. apella* obtained a higher score than *A. macconnelli*, which is considered fully prehensile. Furthermore, Youlatos (1999) argued that the tail of *Cebus* and *Sapajus* must be exposed to important forces during anchoring behaviors. In conjunction with previous anatomical results (Ankel 1962; German 1982; Lemelin 1995; Organ et al. 2009; Organ 2010; Deane et al. 2014), it seems that tail use in *S. apella* might be different but not less demanding than for species suspending themselves, and thus, it raises questions regarding the relevance of the concept of semi-prehensility.

Anatomically speaking, the three species of this study have been demonstrated to present convergence on a wide array of morphological characters such as relative proportion of the tail regions, dimensions and inner structure of the caudal vertebrae, relative size of vertebral processes, size and shape of intervertebral surfaces, chevron bones size and shape, muscles and tendons organization and muscles masses (Dor 1937; Ankel 1962; German 1982; Lemelin 1995; Youlatos 2003; Organ 2007; Organ et al. 2009; Organ 2010; Deane et al. 2014; Zavodszky and Russo 2020).

Beyond this convergent pattern, anatomical differences have been noted between those species. German (1982) noted that the main difference between *Cebus albifrons* and the atelids inspected (*Alouatta villosa* and *Ateles geoffroyi*) happened at the distal end of the tail. In this region, atelids exhibit an increase in the relative width of the proximal transverse processes, whereas *Cebus* does not. A subsequent inspection of caudal musculature in platyrrhines (Lemelin 1995) further identified the ventral flexor muscles originating and inserting on these expanded transverse processes in atelids (i.e., the flexor caudae longus and intertransversarii caudae) and noticed their important relative size compared to the dorsal musculature. Electromyiographical methods showed that the intertransversarii caudae was responsible for a combination of flexion, lateral flexion, and rotation. It has been discussed to play a role in maximizing friction at the tip of the tail as well as to mitigate stresses applied to the intervertebral discs and thus, hypothesized to play an important role in tail suspend behaviors. Furthermore, a study of the size and shape of intervertebral surfaces of caudal vertebrae showed that all prehensile-tailed species tend to have larger articular surfaces than their non-prehensile relatives but that among prehensile species atelids exhibited comparatively higher values than prehensile-tailed cebids (i.e., *Cebus* and *Sapajus*) (Deane et al. 2014). The authors stated that this difference might be the result of the higher stresses generated by tail suspension compared to tripodal postures. The current study, in addition to the aforementioned literature regarding tail-use in *Alouatta* and *Cebus*/*Sapajus*, tends to confirm this hypothesis, establishing suspensory behaviors have a major difference in tail use between these species.

Prehensile-tailed cebids are often described as presenting somewhat of an intermediate state between prehensile and non-prehensile species (Dor 1937; Lemelin 1995; Deane et al. 2014). Nevertheless, Lemelin (1995) argued that this difference is likely due to the independent origin of the prehensile tail between atelids and cebids but that the morphological convergences observed between those species are likely to demonstrate similar constraints exerted on the tail of those species. Furthermore, Organ et al. (2009) demonstrated that the intertransversarii caudae muscle of *Sapajus* was able to generate higher forces than atelids or *P. flavus* in the median region of the tail and interpreted this result as an indicator that *Sapajus* might grasp substrate with a region of the tail more proximally located than other prehensile species present in this study. Our results tend to support this assumption as *S. apella* tends to preferentially use medium to large substrates where contact occurs more proximally along the tail compared to smaller ones.

Regarding *P. flavus*, linking behavior and morphology is more challenging as less data are available. Nevertheless, Youlatos (2003) noted a greater relative expansion of the transverse processes compared to its non-prehensile relatives. This pattern is especially pronounced in the distal end of the tail similarly to what was described in atelids (German 1982; Lemelin 1995). The author thus hypothesized that it might be linked to suspensory behaviors but that behavioral data were lacking to either confirm or infirm it. Tail hindlimb suspend has previously been qualitatively described for *P. flavus* (McClearn 1992), the current study confirms this observation (9.7% of the observed behaviors) as well as tail only suspensory behaviors (24.5% of the observed behaviors), which to our knowledge, were not previously described. Together those results tend to confirm that the convergence between atelids and *P. flavus* might be linked to habits of suspensory behaviors. Myological data are still needed, but the inspection of the intertransversarii caudae muscle (Organ et al. 2009) demonstrated that all prehensile taxa, including *P. flavus*, exhibited higher physiologic cross-sectional area values than their non-prehensile relatives and that these results were mainly explained by differences in muscle mass. It is worth noting that the difference between *P. flavus* and it is non-prehensile relative *Nasua nasua*, was especially striking at the distal end of the tail but less so in the proximal region, leading the authors to postulate that the end of the tail might play a more important role in this species' tail-use. Our results, however, tend to show more frequent use of large substrates (62% of the substrate-use observed) even though grasping on small substrates has been observed as well (12% of the substrate-use observed). More studies regarding both behavior and morphology will be necessary to clarify these results.

The general consistency between our results and the literature describing the positional behaviors and tail use of platyrrhines using other methods confirms the importance of camera trap data for studies interested in long-term surveys of wild animals, as previously argued by Dalloz et al. (2012). In addition to temporal information (Séguigne et al. 2022), these results provided insight into spatial niche partitioning in the tree crown. It would be interesting to compare our results with a similar setup where other potentially competing species are present like representatives of the *Ateles* genus, for example, to explore how this would affect the pattern observed here. Overall, our results add to the body of literature describing positional behaviors in platyrrhines and provide the first quantitative description of such behaviors for wild *P. flavus*. The comparison of the way prehensile tails are used in the three species studied here highlights important differences in the behavioral role of this trait, confirming Meldrum (1998) intuition. Furthermore, including *P. flavus* revealed that this species exhibits a positional repertoire that is more diverse than that of the two primates included in this study. These results emphasize the need to include more species to gain a broader understanding of the similarities and differences in tail-use among prehensile species.

Author Contributions

Arthur Georges Naas: conceptualization (lead), formal analysis (equal), funding acquisition (lead), methodology (equal), project administration (lead), supervision (lead), writing – original draft (equal). **John Bosu Mensah:** conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), writing – original draft (equal), writing – review and editing (equal). **Pierre-Michel Forget:** data curation (lead), investigation (lead), resources (lead), writing – review and editing (equal). **Éric Guilbert:** data curation (lead), investigation (lead), resources (lead), writing – review and editing (equal). **Anthony Herrel:** conceptualization (equal), formal analysis (supporting), investigation (supporting), methodology (supporting), project administration (supporting), supervision (supporting), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All pictures used in this project are available on the database "Effect of anthropogenic activities on wildlife diversity in French Guiana," hosted on the Agouti platform (http://agouti.eu/).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.