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TRABALHO DE CONCLUSÃO DO CURSO DE GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

GUILHERME AKIRA AWANE

COMPORTAMENTO POSICIONAL DOS MACACOS-PREGO-PRETO *Sapajus nigritus* (GOLDFUSS, 1809) (PRIMATES, CEBIDAE) NO CONTEXTO DE FORRAGEIO E ALIMENTAÇÃO EM UM FRAGMENTO FLORESTAL URBANO

Londrina – Paraná

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AWANE, Guilherme Akira. **Comportamento posicional dos macacos-prego-preto *Sapajus nigritus* (Goldfuss, 1809) (Primates, Cebidae) no contexto de forrageio e alimentação em um fragmento florestal urbano.** 2024. 86 fls. Trabalho de Conclusão de Curso (Graduação em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina. 2024.

RESUMO

O comportamento posicional abrange o estudo da morfologia do animal e a interação com o ambiente. Em primatas neotropicais, o comportamento posicional é bem descrito, entretanto, em macacos-prego há uma evidente lacuna de estudos, principalmente no gênero *Sapajus*. A perda de habitat devido ao avanço da urbanização é um dos principais fatores de ameaça às populações de macacos-prego, podendo influenciar seu comportamento posicional. Este estudo teve como objetivo descreve o comportamento posicional de forrageamento/alimentação de um grupo de vida livre de macacos-prego *(Sapajus nigritus*) que habita áreas florestais e urbanas na Universidade Estadual de Londrina. As amostragens foram realizadas com o método *animal focal* de 2 minutos, divididas em 12 pontos com um intervalo de 10 segundos. Em cada ponto registrou-se o comportamento posicional, a área e o substrato de um indivíduo por focal. Os comportamentos diferiram ligeiramente entre as classes de sexo-etárias, com juvenis apresentando maior probabilidade de locomoção com os membros em tensão (Probabilidade = 0,09; RR = 0,10; $p < 0,001$) comparado as fêmeas (Probabilidade = 0,06; RR = 0,07; $p < 0,001$) e machos (Probabilidade = 0,05; RR = 0,05; p = 0,004), enquanto os machos adultos apresentaram maior probabilidade de comportamentos saltatórios (Probabilidade = 0.05; RR = 0.05; p = 0.005), seguido de juvenis (Probabilidade = 0.03; RR = 0.03; $p < 0.001$) e fêmeas adultas (Probabilidade = 0.02; RR = 0.02; $p < 0.001$). O local e o substrato afetaram significativamente os comportamentos posicionais, especialmente a locomoção quadrúpede, com maior probabilidade de ocorrer no substrato terrestre (Probabilidade = 0.90%; RR = 8.45; $p < 0.001$) comparado ao substrato edificado (Probabilidade = 0.79%; RR = 3.99 p = 0.013) e arbóreo (Probabilidade = 0.79; RR = 3.80; p = 0.002) e maior probabilidade de ocorrer nas áreas urbanas comparado aos fragmentos de mata (Urbano: probabilidade = 0.35%; RR = 0.54; $p < 0.001$; Fragmentos de mata: probabilidade = 0.28%; RR = 0.39; $p < 0.001$).

Palavras-chave: comportamento locomotor; comportamento postural; macaco-prego urbano.

AWANE, Guilherme Akira. **Positional behavior in wild black-horned capuchin monkey *Sapajus nigritus* (Goldfuss, 1809) (Primates, Cebidae) while foraging and feeding in na urban forest fragment.** 2024. 86 pgs. Final Dissertation (Biological Sciences Undergraduation) – Londrina State University. Londrina. 2024.

ABSTRACT

Positional behavior has been well studied in many neotropical primate species. However, the positional behavior in capuchin monkeys is still understudied. This knowledge gap is particularly evident for robust capuchins (*Sapajus* sp.). Positional behavior involves the study of the morphology and the environment. Habitat loss due to increasing of urbanization is one of the main threats to capuchin monkey populations, which could influence their positional behavior. This study objective was to describe the foraging and feeding positional behavior of a wild group of black-horned capuchin monkeys (*Sapajus nigritus*) living in forest and urban areas at the State University of Londrina, Brazil. We conducted 2-minute focal-animal samplings, divided in 12 sampling points with a 10 second interval, each sampling point we recorded the positional behavior, area, and substrate of one individual per focal. Probability behaviors differed slightly by sex-age classes, juveniles showing a higher probability of locomotion with limbs in tension (Probability = 0,09; RR = 0,10; $p < 0,001$), compared to adult females (Probability = 0,06; RR = 0,07; $p < 0,001$) and adult males (Probability = 0,05; RR = 0,05; $p = 0,004$), meanwhile adults male show a higher probability of leaping behaviors (Probability = 0.05; RR = 0.05; $p = 0.005$), compared to juveniles (Probability = 0.03; RR = 0.03; $p < 0.001$) and adult females (Probability = 0.02; RR = 0.02; $p < 0.001$). Site and substrate significantly affected the positional behaviors, particularly for quadrupedal cursorial locomotion with a higher probability occurrence in terrestrial substrate (Probability = 90%; RR = 8.45; $p < 0.001$), compared to building substrate (Probability = 79%; RR = 3.99 $p = 0.013$), and arboreal substrate (Probability = 79%; RR = 3.80; $p = 0.002$), and was more likely to be observed in urban areas compared to natural areas (Urban: probability = 35%; RR = 0.54; $p < 0.001$; Natural: probability = 28%; RR = 0.39; $p < 0.001$).

Keywords: locomotor behavior; postural behavior; urban capuchin.

Sumário

1. INTRODUÇÃO

O comportamento posicional é definido como o conjunto de padrões locomotores e posturas que os animais realizam em interação com o ambiente (Prost, 1965), exprimindo a eficácia com a qual o animal se utiliza do seu habitat, seja no forrageio, alimentação ou em evitar a predação (Saunders; Roberts; Thorpe, 2017). Diversos estudos sobre padrões e variações do comportamento posicional foram realizados em primatas neotropicais (Dagosto; Gebo, 1998), envolvendo principalmente: *Ateles* (Cant, 1986; Cant; Youlatos; Rose, 2003; Fontaine, 1990; Fontaine, 1994; Fleagle; Mittermeier, 1980; Youlatos, 2002, 2008;), *Alouatta* (Bezanson, 2006, 2009, 2012; Cant, 1986; Fontaine, 1994; Fleagle; Mittermeier, 1980; Gebo, 1992), *Cacajao* (Fontaine, 1994), *Callicebus* (Lawler et al., 2006), *Chiropotes* (Fleagle; Mittermeier, 1980), *Lagothrix* (Cant; Youlatos; Rose, 2003), *Pithecia* (Fleagle; Mittermeier, 1980) e *Saguinus* (Fleagle; Mittermeier, 1980; Garber; Pruetz, 1994).

Tendências na diferença de tamanho corporal (Fleagle; Mittermeier, 1980; Gebo; Chapman, 1995), interação com o ambiente (Fleagle; Mittermeier, 1980; Lawer *et al*., 2006; Youlatos, 1999) e diferenças intraespecíficas na ontogenia (Bezanson, 2009) foram observadas em relação a comportamentos posicionais distintos. Em relação a ontogenia, estudos observaram que juvenis (*Cebus capucinus* e *Alouatta palliata*) apresentam um repertório posicional mais diverso (Bezanson, 2009), com andar quadrúpede com mais escalada e saltos, e menor frequência de locomoção (Wright, 2007).

Contudo os estudos sobre o comportamento posicional dos primatas da família Cebidae concentram-se em algumas espécies, como em: *Saimiri bolivinensis, Saimiri sciureus* (Fontaine, 1990; Fontaine, 1994; Fleagle; Mittermeier, 1980), *Cebus capucinus, Cebus olivaceus* (Bezanson, 2006, 2009, 2012; Fontaine, 1994; Garber; Rehg, 1999; Gebo, 1992; Wright, 2007; Youlatos, 1998), *Sapajus libidinosus e Sapajus apella* (Hanna *et al.,* 2015; Laird *et al.,* 2022; Wright, 2007; Wright *et al.,* 2019; Youlatos, 1998).

O estudo do comportamento posicional em macacos-prego, buscando compreender os efeitos do ambiente nos traços evolutivos de forrageio e locomoção, é apontado como uma das prioridades de pesquisa neste grupo (Lynch-Alfaro; Izar; Ferreira, 2014). Embora o gênero *Sapajus* (macacos-prego robustos) compreenda oito espécies (*S. nigritus, S. libidinosus, S. apella, S. xanthosternos, S. robustus, S. flavius, S. macrocephalus* e *S. cay* - Martins *et al*., 2023), o repertório posicional é conhecido em apenas duas, *S. apella* (Wright, 2007; Youlatos, 1998) e *S. libidinosus* (Hanna *et al.,* 2015; Laird *et al*., 2021; Wright *et al.,* 2019).

As espécies do gênero *Sapajus,* segundo a *International Union for Conservation of Nature* – IUCN, compartilham das mesmas ameaças, a expansão urbana e a perda de habitat pela conversão em matriz agrícola (Canale *et al*., 2013; Mota *et al*., 2018; Ludwig *et al*., 2022; Martins *et al*., 2022). Existem evidências de que a expansão urbana, a fragmentação e a perda de habitat afetam as atividades de diferentes grupos de animais (Gaynor *et al*., 2018; Gallo *et al*., 2022), o orçamento de atividade comportamental (Back; Suzin; Aguiar, 2019; Gutierres *et al*., 2023; Lousa *et al*., 2022), a área de vida e o uso do espaço (Patterson *et al*., 2019) e a prevalência na matriz urbana em relação a sítios de alimentações antrópicos (Patterson *et al*., 2018).

No que diz respeito aos primatas nas florestas tropicais, supõe-se que a expansão urbana seja um catalisador para a adoção de substratos terrestres, limitando a cobertura vegetal a pequenas manchas, resultando em menor quantidade de alimentos ou de menor qualidade (Eppley *et al*., 2022). A mudança no uso do espaço relacionada com o forrageio foi observada em macacos urbanos, cuja prevalência em determinados locais está relacionada com a disponibilidade de alimentos de origem antrópica (macacos vervet *Chlorocebus pygerrythrus*– Patterson *et al*., 2019).

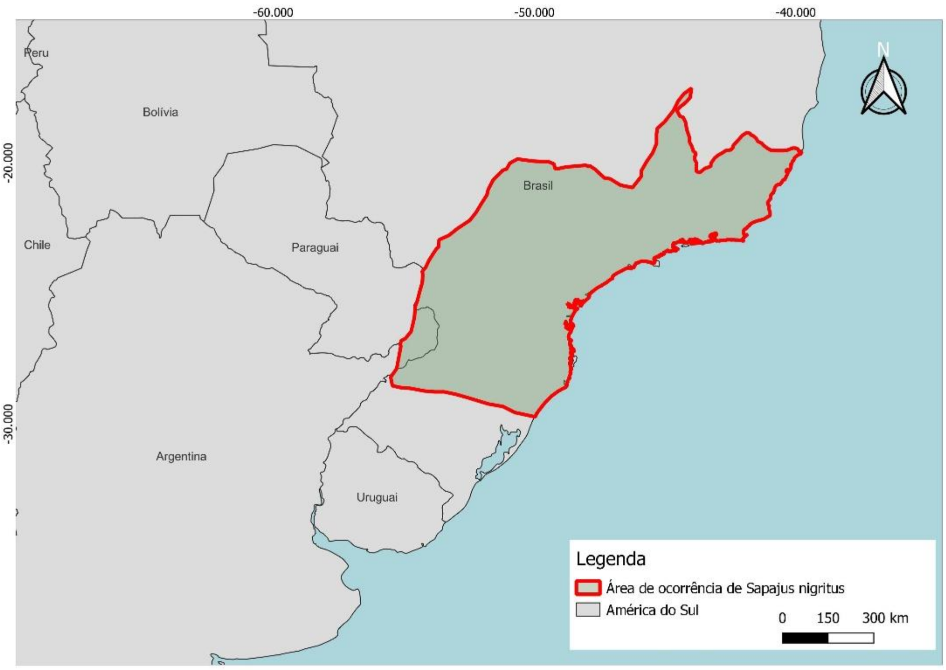
Estudos de comportamentos posicionais podem servir como ferramenta para conservação, pois permitem compreender como e quais as limitações que esse ambiente modificad, impõe a esses animais, auxiliando no entendimento a respeito da plasticidade comportamental dos animais em ambiente urbano (Perodaskalaki *et al*., 2023).

A espécie de *Sapajus nigritus*

Os macacos-prego-pretos (*Sapajus nigritus*) segunda a lista vermelha de espécies ameaçadas da IUCN essa espécie está classificada como “Quase ameaçada”, com tendência de declínio, tem entre suas principais ameaças a redução e perda de habitat, por meio degradação, incêndios, aumento das malhas rodoviárias e da matriz agrícola (Ludwig *et al*., 2022).

S. nigritus é uma espécie endêmica da Mata Atlântica e encontra-se distribuído pela costa brasileira e Argentina, nas províncias do Iguaçu e Missiones (figura 1).

Figura 2: Mapa da área de ocorrência de *Sapajus nigritus*.



Fonte: próprio autor.

Possuem corpo robusto com pelagem escura e na região da cabeça, possuem aglomerados de pelos que caracterizam seu nome popular de macaco-prego-preto ou macaco-prego dos tufos negros. A identificação individual desses animais pode ser realizada a partir de características como o formato do rosto, tamanho corporal, coloração da pelagem, cicatrizes, forma da cauda, forma do topete e ausência de membros (Izawa, 1980). O tamanho corporal e presença de topetes podem ser utilizados para agrupar infantes, juvenis e adultos (figura 2) (Resende; Ottoni; Fragaszy, 2008), e os sexos podem ser identificados a partir da visualização das genitálias (Fragaszy; Visalberghi; Fedigan, 2004).

Figura 2: Identificação das classes sexo-etárias de alguns indivíduos do bando da Universidade Estadual de Londrina (fotografia a – Rodrigo de Sá; fotografia b-f – Guilherme Akira Awane. a) Billy (Macho Juvenil) – início do desenvolvimento do topete característico dos indivíduos do sexo masculino; b) Billy (Macho Adulto) – presença de topete com separação evidente; c) Piper (Fêmea Adulta) – presença de topete sem separação evidente; d) Diferença de tamanho corporal entre a fêmea adulta Bailey e o macho adulto Alfa; e) Diferença do tamanho corporal entre macho adulto Alfa e juvenil; f) Diferença de tamanho corporal entre a fêmea adulta Zoey e juvenil.

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Os macacos-prego-pretos que habitam no campus da Universidade Estadual de Londrina, são uma população selvagem de vida livre, e como estão constantemente em contato com o ambiente urbano, essa população pode servir de modelo para compreender como o ambiente urbano possa estar afetando os comportamentos posicionais, já que até o momento, não há registro na literatura a respeito do comportamento posicional de *S. nigritus* em ambiente urbano.

Sendo assim, o objetivo deste estudo foi avaliar o comportamento posicional dos macacos-prego-preto *S. nigritus* no campus da Universidade Estadual de Londrina. Foram testadas as seguintes hipóteses: i) Considerando a tendência de adoção de comportamentos terrestres em ambientes urbanos por primatas (Eppley *et al*., 2022), espera-se que o ambiente urbano acarrete em mudança no uso do substrato, com menor probabilidade de comportamentos suspensórios nos ambientes urbanos comparado aos fragmentos de mata presentes no campus; ii) Os comportamentos posicionais variam de acordo com o sexo e a idade independente do tipo de ambiente (Bezanson, 2009; Wright, 2007), sendo: (a) que os jovens exibirão mais comportamentos locomotores, como saltos, locomoção bípede e locomoção com membros em tensão, do que locomoção cursorial quadrúpede em comparação com os adultos, (b) e o comportamento suspensório variará entre os adultos, com maior probabilidade de comportamento suspensório nas fêmeas.

2. REVISÃO BIBLIOGRÁFICA

Comportamento Locomotor

Os comportamentos locomotores ou padrões locomotores podem ser definidos segundo Ripley (1967) como a variedade de habilidades complexas que são aprendidas e treinadas. Prost (1965) também define esses comportamentos locomotores como um processo, não apenas um deslocamento do organismo, mas uma ação orgânica que ocorre durante o deslocamento do organismo. Partindo das duas definições, os comportamentos locomotores podem ser entendidos como uma variedade de habilidades complexas que são desenvolvidas e ocorrem durante o processo de deslocamento do organismo.

O estudo desses comportamentos, particularmente em primatas, está relacionado ao estudo de formas vivas a fim de se compreender a história evolutiva de espécies extintos e do homem (Dagosto; Gebo, 1998; Washburn, 1950). Esses comportamentos podem ser divididos em diferentes tipos locomotores como: quadrupedalismo, saltos, escalada, bipedalismo, braquiação e nodopedalia (Fleagle; Mittermeier, 1980; Fontaine, 1990; 1994; Ripley, 1967).

A categoria de braquiação devido a várias definições muito abrangentes geraram o estado de confusão dentro dos comportamentos locomotores (Prost, 1965; Tuttle, 1975). Devido à falta de dados detalhados em espécimes selvagens conclusões acerca dos padrões locomotores foram baseadas em espécimes em cativeiro e em dados qualitativos e anedotas (Dagosto; Gebo, 1998), que não necessariamente representam todo repertório locomotor da espécie (Ripley, 1967).

A braquiação foi definida primeiramente como um “elaborado complexo comportamental e anatômico, com cada detalhe essencial compartilhado entre o homem e os macacos antropoides” (Washburn, 1950). Avis (1962) corrobora e classifica os macacos antropoides como braquiadores, incluindo os chimpanzés e gorilas. Schaller (1963) contrariamente não classifica os gorilas como braquiadores e afirma que todos os antropoides são essencialmente escaladores quadrúpedes. Remis (1998) classifica a locomoção dos gorilas com escalada, nodopedalia quadrúpedes e mais raramente bípedes. Os chimpanzés, apesar de demonstrarem diferenças no seu padrão de locomoção de acordo com o seu desenvolvimento (Sarringhaus; MacLatchy; Mitani, 2014), apresenta o padrão locomotor dominante, sendo quadrupede com nodopedalia (Hunt, 1990) e escalada quadrúpede (Doran, 1993).

Comportamento Posicional

O comportamento posicional surge conceitualmente como uma tentativa de resolução do estado de desordem da classificação dos comportamentos locomotores. É definido por Prost (1965) em duas etapas: o comportamento a relação entre os indivíduos e o ambiente, enquanto o posicional engloba os comportamentos locomotores e comportamentos posturais que são eventos alternativos, de maneira que o animal está ou em movimento ou parado exibindo uma postura. No estudo posicional, a integração do animal com seu ambiente permite avaliar como ocorre a utilização do habitat, sucesso no forrageio, o ato de evitar predação e estratégias reprodutivas (Bezanson, 2017; Sarringhaus; MacLatchy; Mitani, 2014).

Uma das problemáticas iniciais do estudo do comportamento posicional foram os poucos estudos produzidos (Dagosto; Gebo, 1998) e a falta de uma padronização na terminologia (Dagosto; Gebo, 1998; Hunt *et al*., 1996; Ripley, 1967). A primeira sistematização foi baseada em classificações em modos e sub-modos. Os modos são grupos compilados de comportamento, sendo definidos de maneira funcional de acordo com anatomia e atributos mecânicos utilizados, enquanto os sub-modos são os comportamentos que são variações de um modo (Hunt *et al*., 1996; Saunders; Roberts; Thorpe, 2017).

Desde então, estudos de campo padronizados têm sido produzidos, apresentando a descrição dos comportamentos (i.e, o repertório posicional ou etograma), o contexto comportamental (e.g. forrageio/alimentação, deslocamento e descanso) e uso do substrato (Bezanson, 2017). A maior parte dos estudos relacionados a comportamento posicional produzidos até 2016 são relacionados a primatas do Novo Mundo, apresentando uma diversidade ainda maior de questões, como ontogenia, interação com habitat e relação a massa corporal (Bezanson, 2017; Dagosto; Gebo, 1998).

Diferença da massa corporal

Os Primatas apresentam diferentes repertórios posicionais, que entre outras variáveis, são explicados pela massa corporal, representada pelo tamanho corporal em alguns casos (Cant, 1992; Druelle; Aerts; Berillon, 2016; Fleagle; Mittermeier, 1980; Gebo; Chapman, 1995; Zhu *et al*., 2014).

Nos primatas de novo mundo, aqueles com maior tamanho corporal exibem maiores taxas de comportamentos de escaladas e menores de comportamentos saltatórios quando comparados com primatas de menor tamanho corporal (Fleagle e Mittermeier, 1980). Essa mesma tendência não foi encontrada em primatas do velho mundo, já que as espécies com menor tamanho corpóreo realizam mais comportamentos de escalada e menos comportamentos saltatórios, enquanto as de maior tamanho realizam mais comportamentos saltatórios (Gebo; Chapman, 1995).

Essa diferença pode estar relacionada aos estratos onde os comportamentos foram executados. Os primatas do novo mundo executando comportamento saltatórios no sub-bosque e comportamentos quadrúpedes no meio do dossel (sendo esses os estratos com espaços mais descontínuos). Os primatas do velho mundo executaram mais comportamentos saltatórios no meio ou topo do dossel (Gebo e Chapman, 1995). Assim o tamanho corporal é uma variável que pode explicar os comportamentos posicionais das espécies, mas não é isolada da influência do ambiente em relação ao repertório posicional.

Os estudos sobre tamanho corporal e comportamento posicional eram realizados de maneira interespecíficas com espécies simpátricas (Fleagle; Mittermeier, 1980; Gebo; Chapman, 1985). Contudo, outros estudos com base na ontogenia surgem para observar as potenciais diferenças entre as classes etárias de indivíduos de uma mesma espécie, com foco na diferença de tamanho corporal nos estágios de desenvolvimento dos indivíduos e sua relação com o repertório posicional que eles apresentam (Bezanson; Morbeck, 2013; Lawler, 2006).

Ontogenia

O comportamento posicional enquanto integração entre morfologia e o ambiente desempenha um papel importante durante toda a vida do indivíduo e sua história de vida (Bezanson, 2009; Morbeck, 2013; Doran, 1992). A ontogenia do comportamento posicional permite o entendimento sobre a adaptação dos movimentos, em uma abordagem de relação funcional entre crescimento e mudanças no comportamento com as demandas impostas pelo ambiente (Lawler, 2006).

Diferenças nos comportamentos locomotores são observadas entre as classes etárias de chimpanzés, com juvenis exibindo um repertório locomotor marcado com comportamentos de suspensão e conforme envelhecem modificam seu repertório exibindo mias comportamentos quadrúpedes (Doran, 1992; Sarringhaus; MacLatchy; Mitani, 2014). Transição similar foi observada nos cairaras (*Cebus capucinus*) e nos bugios (*Alouatta palliata*), com os indivíduos imaturos modificando seu repertório posicional para comportamentos similares aos dos adultos durante seu amadurecimento (Bezanson, 2009).

Nos macacos-prego, os juvenis demonstram maiores frequências de escalada e salto, mas menores frequências de andar quadrúpede quando comparados aos adultos durante o forrageio e deslocamento (Bezanson, 2009; Wright, 2007). Juvenis brincam mais que os adultos. Durante as brincadeiras acabam exibindo um repertório posicional mais diverso, contudo, mesmo quando não estão brincando juvenis tendem a usar outros padrões de locomoção, ao invés de locomoção cursorial quadrúpede (padrão locomotor mais comum em adultos), relacionados ao treino de flexibilidade nos primatas arbóreos (Fontaine, 1994).

Diferenças entre os sexos

A diferença de massa corporal de machos e fêmeas adultos influencia o repertório posicional e uso do ambiente em diferentes substratos (Fragaszy, 1990; Gebo, 1992; Wright et al., 2019; Zhu et al., 2014). Esse uso dos substratos pode estar associado com diferenças de nicho intraespecíficas com a finalidade de evitar competição entre fêmeas e machos adultos (Williamson et al., 2021). Dessa forma, machos passam mais tempo no substrato terrestre devido a sua maior massa corporal, e fêmeas utilizam mais frequentemente o substrato arbóreo (Fragaszy, 1990). Portanto, é esperado que fêmeas demonstrem mais comportamentos suspensórios que os machos.

Interação com habitat

O ambiente influencia o repertório posicional dos primatas por meio do seus diferentes estratos e substratos, onde um mesmo ambiente pode ser percebido de maneira diferente por diferentes primatas. O mesmo espaço pode ser mais ou menos contínuo de acordo com o tamanho corporal de cada primata, resultando em comportamentos distintos em cada espécie para superar os desafios do ambiente (Fleagle; Mittermeier, 1980; Gebo; Chapman, 1985).

No caso de primatas, argumenta-se que animais menores percebem o ambiente com mais espaços descontínuos, de maneira que usam os saltos para superar essa descontinuidade do ambiente, enquanto primatas maiores não estão sujeitos as mesmas desconexões no ambiente que os animais menores, assim resultando em outras formas de se locomover no ambiente (Fleagle; Mittermeier, 1980).

Youlatos (1999) estudando seis espécies simpátricas no Equador, observou que os macacos de menor porte exploravam os estratos mais baixos da cobertura vegetal, enquanto macacos maiores exploraram estratos mais altos, chegando ao estrato emergente. Uma das explicações está no menor risco de predadores aéreos nos estratos inferiores, preferidos pelas espécies menores, enquanto os macacos de maior porte podem explorar os estratos mais altos e por possuírem maior porte, estão menos suscetíveis a predação. Assim como Fleagle e Mittermeier (1980), Youlatos (1999) observou que as espécies de maior porte tendem a exibir mais comportamento locomotor quadrupede e escalada, mas pondera que espécies de tamanhos intermediários como macacos-prego (*Cebinae*) e parauacu (*Pitheciinae*) utilizam saltos tanto quanto pontes pronógradas.

Em *Callicebus,* primatas do novo mundo, também há diferenças no comportamento posicional em relação ao estrato utilizado, sendo que *C. brunneus* ocupa os estratos mais baixos e apresenta mais comportamentos saltatórios curtos e postura vertical, enquanto *C. torquatus* permanece mais nos estratos superiores e apresenta maiores taxas de comportamento locomotor quadrúpede e taxas muito baixas da postura vertical (Lawer *et al*., 2006). A permanência de *C. brunneus* em estratos mais baixos é explicada pela competição interespecífica, já que apresentam pequeno porte, e devido a composição do grupo que geralmente não ultrapassa quatro indivíduos, assim acabam utilizando recursos distribuídos horizontalmente (e.g. folhas) nesse estrato. Assim essa espécie se mantém em um ambiente mais descontínuo com maior necessidade de saltos a curtas distâncias. Enquanto *C. torquatus*, explora os recursos distribuídos verticalmente (e.g. frutos) nesses ambientes, apresentando mais comportamento locomotores quadrúpedes (Lawer *et al*., 2006).

Primatas do Novo Mundo

Diversos estudos sobre o comportamento posicional foram realizados com os macacos do Novo mundo, como nos: atelídeos, *Ateles* (Cant, 1986; Cant; Youlatos; Rose, 2003; Bergeson, 1998; Fontaine, 1990; Fontaine, 1994; Fleagle; Mittermeier, 1980; Johnson; Shapiro, 1998; Youlatos, 2002, 2008), *Alouatta* (Bergeson, 1998; Bezanson, 2006, 2009, 2012; Cant, 1986; Fontaine, 1994; Fleagle; Mittermeier, 1980; Gebo, 1992; Johnson; Shapiro, 1998; Prates; Bicca-Marques, 2008; Youlatos, 1998) e *Lagothrix* (Cant; Youlatos; Rose, 2003); piteciídeos, *Pithecia* (Fleagle; Mittermeier, 1980), *Chiropotes* (Fleagle; Mittermeier, 1980), *Callicebus* (Lawer *et al*., 2006) *e Cacajao* (Fontaine, 1994); calitriquídeos, *Saguinus* (Fleagle;

Mittermeier, 1980; Garber; Pruetz, 1994); cebídeos, *Saimiri* (Boinski; Fragaszy 1989; Fontaine, 1990, 1994; Fleagle; Mittermeier, 1980; Johnson; Shapiro, 1998; Youlatos, 1999), *Cebus* (Bergeson,1998; Bezanson, 2006, 2009, 2012; Fontaine, 1994; Garber; Rehg, 1999; Gebo, 1992; Johnson; Shapiro, 1998; Youlatos, 1998, 1999) e *Sapajus* (Hanna *et al*., 2015; Laird *et al*., 2021; Wright, 2007; Wright *et al*., 2019; Youlatos, 1998).

Dentre os macacos-prego (gêneros *Sapajus* e *Cebus*) a maioria dos estudos foram realizados com os macacos do gênero *Cebus,* em particular com *C. capucinus* (Bergeson,1998; Bezanson, 2006, 2009, 2012; Fontaine, 1994; Garber; Rehg, 1999; Gebo, 1992; Johnson; Shapiro, 1998), enquanto estudos envolvendo os gêneros *Sapajus* são restritos a duas espécies: *S. apella* (Wright, 2007; Youlatos, 1998); *S. libidinosus* (Hanna *et al*., 2015; Laird *et al*., 2021; Wright *et al*., 2019).

O repertório posicional da família Cebidae (gêneros *Cebus*, *Sapajus* e *Saimiri*) envolvem comportamentos suspensórios, locomoção quadrúpede, escalada e saltos (Bergeson, 1998; Bezanson, 2006, 2009, 2012; Boinski; Fragaszy 1989; Fleagle; Mittermeier, 1980; Fontaine, 1990, 1994; Garber; Rehg, 1999; Gebo, 1992; Hanna *et al*., 2015; Johnson; Shapiro, 1998; Laird *et al*., 2021; Wright, 2007; Wright *et al*., 2019; Youlatos, 1998, 1999).

Os macacos do gênero *Saimiri* possuem menor tamanho corporal dentro da família Cebidae, variando de 600-992g dependendo da espécie (Boinski, *et al*., 2002; Fleagle; Mittermeier, 1980). Preferencialmente são encontrados no sub-bosque (Boinski; Fragaszy, 1989; Fleagle; Mittermeier, 1980), e seu repertório posicional é dominado por locomoção quadrúpede, seguido de saltos, escalada (Boinski; Fragaszy, 1989; Fleagle; Mittermeier, 1980; Fontaine, 1990, 1994; Youlatos, 1999) e locomoção quadrúpede com membros em tensão (Fontaine, 1990, 1994;

Johnson; Shapiro, 1998). Comportamentos suspensórios são pouco ou não são observados (Boinski; Fragaszy, 1989; Fontaine, 1990, 1994; Johnson; Shapiro, 1998), onde a suspensão pela cauda nunca foi registrada, sendo utilizada apenas para equilíbrio do corpo (Boinski; Fragaszy, 1989; Fontaine, 1990, 1994; Johnson; Shapiro, 1998).

Os macacos-prego (gêneros *Cebus* e *Sapajus*) são descritos na literatura como primatas quadrúpedes arbóreos, que apresentam em seu repertório postural e locomotor, saltos e posturas suspensórias. Assim como os demais primatas neotropicais (Platyrrhini) possuem uma cauda semi-preênsil, que, aparentemente evoluiu independentemente no ancestral comum dos Atelidae e no ancestral comum dos *Cebus* e *Sapajus* (Garber; Rehg, 1999). A cauda semi-preênsil nos macacos-prego é utilizada como um quinto membro e como suporte em posturas suspensórias, auxiliando na distribuição de massa corporal em determinados contextos, como o forrageio (Bezanson, 2012).

Estudos comparativos entre *Cebus* e *Sapajus* (Wright, 2007) mostraram diferenças nos padrões locomotores, sendo que *Sapajus* exibiram um padrão de locomoção mais lento, como andar quadrúpede, enquanto *Cebus* exibiram um padrão de locomoção mais rápido, envolvendo comportamentos posicionais como correr quadrúpede, andar saltitante e saltos (Wright, 2007).

Outro estudo comparando *Sapajus apella* e *Cebus olivaceus* ocorrendo de forma simpátrica (Youlatos, 1998), não evidenciou diferenças significativas nos padrões de locomoção, com ambas as espécies utilizando andar e correr quadrúpede, escalada e saltos. Contudo, *S. apella* apresentam o comportamento *sentar* em uma frequência maior que *C. olivaceus* no contexto de alimentação e forrageio. A maior frequência do comportamento posicional *sentar* durante o forrageio e alimentação em *Sapajus* provavelmente relaciona-se com adaptações crânio-dentais e pós-craniais que permitem explorar alimentos mais duros e resistentes (Youlatos, 1998; Wright, 2007). Outra possibilidade é que essa diferença no gênero *Sapajus* se dê pela estratégia de forrageio, que é feita de maneira mais intensa em uma menor área (Wright, 2007). Contudo ainda carecem estudos a respeito do repertório posicional e a interação dessas espécies com o ambiente, para melhor compreensão acerca do comportamento posicional.

Comportamento posicional no contexto urbano

O estudo do repertório posicional em ambientes fragmentados e urbanos é uma forma importante de seu avaliar a influência do meio e seus possíveis efeitos, já que atualmente os processos de fragmentação e expansão urbana colocam em risco diversas espécies de mamíferos (Rockström *et al*., 2009), entre eles os primatas (Estrada; Garber; Chaudhary, 2020; Estrada *et al*., 2017).

Os primeiros estudos nestes ambientes são recentes e foram com esquilos (*Funambulus pennantii* - Perodaskalaki *et al*., 2023) e com a caturrita, um psitacídeo (*Myiopsitta monachus* - Granatosky *et al*., 2022). Em esquilos, foi visto uma maior preferência pelo substrato artificial (origem urbana) em contextos de forrageio e alimentação, e maior taxa de comportamentos quadrúpedes no mesmo substrato. Já em caturritas, foi observada uma maior diversidade de comportamentos posicionais no ambiente urbano. Contudo, para primatas nesse contexto, os estudos são ausentes.

Apesar da existência de estudos em outros contextos, como orçamento de atividades envolvendo macacos do velho e do novo mundo em espaço urbano (*Sapajus nigritus;* Gutierres *et al*., 2023; *Sapajus* sp*.;* Back; Suzin; Aguiar, 2019; Suzin et al., 2017; *Semnopithecus entellus;* Rahman et al., 2015), nesses estudos foram observadas algumas particularidades quanto ao comportamento. No estudo de macacos do novo mundo envolvendo *Sapajus,* foi observado um alto investimento no contexto comportamental de deslocamento, menor atividade de alimentação e menor frequência de comportamentos de descanso, sendo esses diretamente afetados pela alimentação ou recursos antrópicos (Back; Suzin; Aguiar, 2019; Gutierres *et al.*, 2023). Enquanto para macacos do velho mundo, em *Semnopithecus entellus* foi observado uma prevalência maior dos macacos no substrato terrestre em espaços urbanos, associada a alimentação antrópica (Rahman et al., 2015). Contudo, até então, não há registro na literatura de estudos a respeito do comportamento posicional de primatas em ambiente urbano, sendo escasso o conhecimento sobre os efeitos entre o comportamento posicional e a ambiente.

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3. ARTIGO

Anthropogenic effects on the positional behavior of the southern black-horned capuchin monkey (*Sapajus nigritus*).

Abstract

Positional behavior of capuchin monkeys still understudied. This knowledge gap is particularly evident for the *Sapajus* genera. Habitat loss due to the advance of urbanization is one of the main threats to capuchin monkey populations, but that also could influence their positional behavior. This study describes the foraging and feeding positional behavior of a wild group of black-horned capuchin monkeys (*Sapajus nigritus*) living in forest and urban areas at the State University of Londrina, Brazil. The following hypothesis were tested: i) The urban area leads to a shift in the use of the terrestrial substrate. ii) The positional behaviors vary across sex-age classes. We conducted 2-minute focal-animal samplings, divided in 12 sampling points with a 10 second interval, for each sampling point we recorded the positional behavior, area and substrate of one individual per focal. Probability behaviors differed slightly by sex-age classes. Site and substrate significantly affected the positional behaviors, especially for quadrupedal cursorial locomotion was more likely to be observed in urban areas.

Keywords: urban; locomotor behavior; postural behavior; urban capuchin.

Introduction

The study of positional behavior in primates consists of the perception of the interaction between postures and locomotor patterns within the environment (Prost, 1995). Given this behavior-environment interaction, field studies are fundamental for the comprehension of species' positional repertoire, frequencies, as well as behavioral contexts and substrates in which each behavior is observed/displayed (Bezanson & Morberck, 2013; Cant, 1986; Cant et al., 2003; Dagosto & Gebo, 1998; Fleagle & Mittermeier, 1980; Fontaine, 1990; Garber & Pruetz, 1995; Morbeck, 1977; Wright, 2007; Wright et al, 2019; Youlatos, 1998, 2008).

Studies on several platyrrhine and catarrhine primates unfold general and species-specific components of postures and locomotor patterns. It is evident that ecological, behavioral, and morphological factors affect primate's locomotor behavior. For instance, locomotor repertoire (Fleagle & Mittermeier, 1980), feeding niche (Rosenberger, 1992), age classes (Bezanson, 2009; Fontaine 1994, Wright, 2007), sexual dimorphism and substrate use are well-evidenced trends that affects the primate's postural behavior (Gebo, 1992; Fragaszy, 1990).

Age differences have been described between juveniles and adults. The positional behavior of juveniles differs from that of adults, but at some point, begins to resemble it (Bezanson, 2009). Juveniles play more than adults, therefore end up showing a positional repertoire more diverse. However, even when they are not playing, the juveniles tend to use other locomotion patterns than quadrupedal cursorial locomotion related to a flexibility training to arboreal primates (Fontaine, 1994). In capuchin monkeys, juveniles engage more in climbing and leaping but less in walking compared to adults during foraging and traveling contexts (Bezanson, 2009; Wright, 2007).

The positional behaviors displayed are also influenced by sex-class (Gebo, 1992), as males and females can differ in substrate use, that can be associated with intraspecific niche differentiation, avoiding competition between males and females (Williamson et al., 2021). The difference in substrate use is related to difference in positional behavior and body mass, as males (i.e. heavier individuals) spent more time on the ground compared to females (i.e. lighter individuals) (Fragaszy, 1990). Therefore, is expected that females will engage in more suspensory behaviors than males.

Platyrrhine monkeys positional behavior has been described for several genera such as *Ateles* (Cant, 1986; Cant, Youlatos & Rose, 2003; Youlatos, 2002, 2008), *Cacajao* (Fontaine, 1994), *Alouatta* (Bezanson, 2006, 2009, 2012; Cant, 1986; Fontaine, 1994; Fleagle; Mittermeier, 1980; Gebo, 1992), *Callicebus* (Lawler et al., 2006), *Cebus* (Youlatos, 1999; Bergeson, 1998; Bezanson, 2009; Garber & Rehg, 1999; Gebo, 1992; Johnson & Shapiro, 1998; Wright, 2007; Youlatos, 1998), *Chiropotes* (Fleagle; Mittermeier, 1980); *Lagothrix* (Cant et al., 2003), *Pithecia* (Fleagle; Mittermeier, 1980), *Saguinus* (Garber & Pruetz, 1994), and *Sapajus* (Fleagle & Mittermeier, 1980; Gebo, 1992; Wright, 2007; Wright et al., 2019;

Youlatos, 1998, 1999). Regarding to *Sapajus*, positional behavior studies have focused on only two species: *S. apella* and *S. libidinosus*, while the other seven species are still poorly studied.

All species in the genus *Sapajus* are currently showing a trend of population decline. Their conservation status ranges from Near Threatened to Critically Endangered (IUCN, 2023). The main threats to population are urban expansion, habitat fragmentation and disconnection, and predation by exotic species (Canale et al., 2013; Mota et al., 2018; Ludwig et al., 2022; Martins et al., 2022). These impacts affect several animal taxa activity periods (Gaynor et al., 2018; Gallo et al., 2022), behavioral time budget (Back, J.P.; Suzin, A., Aguiar, L.M., 2019; Gutierres et al., 2023; Lousa et al., 2022), home range and space use patterns (Patterson et al., 2019), prevalence in urban matrix (Patterson et al., 2018), and may be drivers of positional behavior plasticity and adaptation. The study of positional behaviors in capuchin monkeys could clarify how environmental factors influence physical and physiological traits such as feeding, foraging, locomotion and habitat use (Lynch-Alfaro et al., 2014).

Regarding to primates in tropical forests, urban expansion is hypothesized to be a catalyst for the adoption of terrestrial substrates by limiting vegetation cover to small patches, resulting in less or lower quality food (Eppley et al., 2022). This shift in spatial exploration related to foraging has also been observed in other urban monkeys, whose prevalence in certain locations is related to anthropogenic food availability (Lousa et al., 2022; Patterson et al., 2019).

In the present study, we investigated black-horned capuchin monkeys' (*Sapajus nigritus*) foraging and feeding positional behavior repertoire. The group lives in forest fragments and urban areas, an environmental context not yet described in the positional behavior literature for the genus. We aim to determine whether there are differences in positional behavior associated to sex-age and location (Bezanson, 2006; Eppley et al., 2022; Gebo, 1992; Fontaine, 1994; Fragaszy, 1990). We hypothesize that: i) The urban area leads to a shift in the use of the terrestrial substrate, so we predict lower probability of suspensory behavior on urban environments than forest fragments. ii) The positional behaviors vary across sex-age classes, so we predict: (a) that juveniles will display more probability to locomotors behaviors, like leaping, bipedal and locomotion with limbs in tension, than quadrupedal cursorial locomotion compared to adults, (b) and suspensory behavior will vary between adults, with more probability to suspensory behavior in females.

Methods

Study site and group

The study was conducted in the State University of Londrina, municipality of Londrina, state of Paraná, Brazil (23º19' 40"S 51º12'08"W). The black-horned capuchin group (*Sapajus nigritus*) lives on the university campus, in a limited home range area that encompasses urban, farmland (crop and livestock production sites) and natural environments (Lorenzo, 2018). The campus consists in 235 ha, composed of urban areas (i.e. buildings, pavements, parking lots, and tree conglomerates), Atlantic Forest fragments (20 hectare Horto Florestal and 3 hectare Mata da Capela), and pasture and crop areas (i.e. Fazenda Escola) (Gutierres et al., 2023). These areas are connected to forest fragments and tree patches by habitat and functional corridors (Figure 1). Despite its heterogeneity, the habitat forms a continuum that facilitates the movement of the group between different areas (Leite, 2012; (Rudnick et al., 2012).

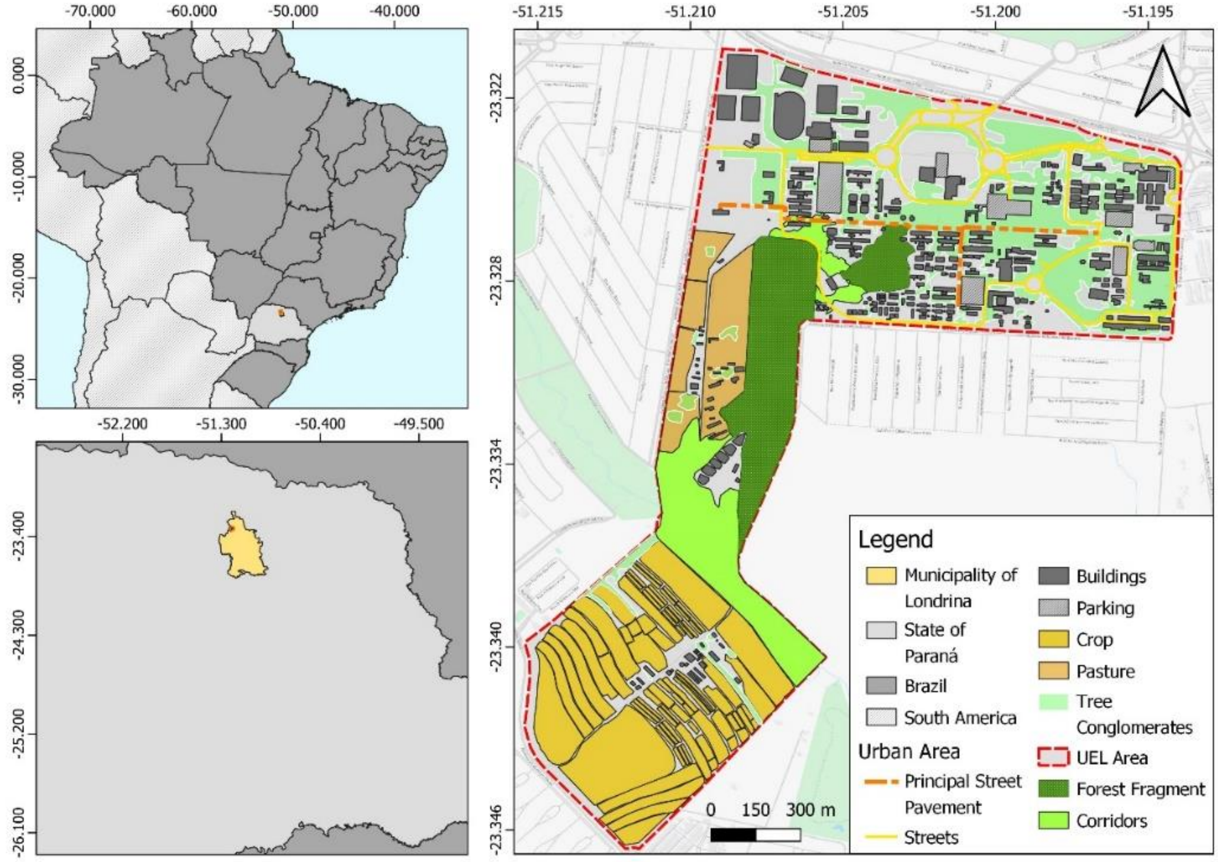

Figure 1. Campus of the State University of Londrina (UEL), State of Paraná, southern Brazil, urban areas, forest fragments, and corridors.

During the study, the group consisted of approximately 39 individuals (3 adult males, 12 adult females, 18 juveniles and 6 infants). Individual sex-age classes identification was based on facial characteristics (Izawa, 1980). Infants were not included in this study because they do not feed or forage alone (Table 1).

Table 1. Individuals and sex-age classes of the *Sapajus nigritus* group in the campus of the State University of Londrina (UEL), State of Paraná, southern Brazil.

Nº	Name	Sex-age class
1	Alfa	Adult Male
2	Billy	Adult Male
3	Tom	Adult Male
4	Alt	Adult Female
5	Bailey	Adult Female
6	Brown	Adult Female
7	Dixie	Adult Female
8	Feia	Adult Female
9	Jolie	Adult Female
10	Juca	Adult Female
11	Lucas	Adult Female
12	Oz	Adult Female
13	Piper	Adult Female
14	Zee	Adult Female
15	Zoey	Adult Female
16	Goo	Juvenile III
17	Rob	Juvenile III
18	Sol	Juvenile III
19	Uatu	Juvenile III
20	Drop	Juvenile III
21	Maul	Juvenile II
22	Pirita	Juvenile II
23	Pitt	Juvenile II
24	Visa	Juvenile II
25	Checks	Juvenile I
26	Choco	Juvenile I
27	Clone	Juvenile I
28	Fly	Juvenile I
29	Hex	Juvenile I
30	Jess	Juvenile I
31	Schino	Juvenile I
32	Nose	Juvenile I
33	Astra	Juvenile I

Capuchin monkeys had easy access to several environments in the campus. Due to these dynamics, the group would not only feed on natural resources in forest fragments but feed on crops, (i.e corn - *Zea mays*) and frequently interact with humans and anthropized environments while foraging. In urban areas, humans rarely provide food directly to monkeys, and the capuchins were constantly foraging and feeding on trash cans (Gutierres et al., 2023). Other anthropogenic food sources are also accessed by the capuchins. These include the feed for the university's livestock and the eggs of chickens located in experimental fields nearby Horto Florestal forest fragment (Figure 1).

Data Collection

We carried out the study in two stages. In the first one, we conducted a behavioral observation period from January to July 2021, with the aim of produce a positional behavior ethogram.

Behaviors were video recorded through direct observation with focal animal sampling (Altmann, 1974; Bateson; Martin, 2). Focal samplings duration varied according to the contact time with individuals, as we record each individual until we lost visual contact. To assess positional behaviors observed in the group, videos were watched by G.A.A and positional behaviors observed during foraging and feeding were identified according to ethograms in Fontaine (1990, 1994). Digital illustrations of these behaviors were elaborated with video frames as molds using a Wacom CTL-470 digitizer tablet and the AutoDesk SketchBook program, following a technical standard (Youlatos, 2002; Supplementary material S1).

In the second stage, we collected data from the positional behavior displayed by the group, from August 2021 to July 2022. Observations were conducted for two to four hours per day, three times per week. We conducted focal animal with instantaneous sampling (Altmann, 1974; Martin & Bateson, 2007). Individual focal sample duration was two minutes, and each sample comprised of 12 sampling points split every 10 seconds for instantaneous sampling.

To define the focal individual, we randomly selected five names out of 33 monkeys, and in the field, we looked for one of the five monkeys that were foraging or feeding to start the focal sampling. We sorted individuals in order to reduce the possible individual autocorrelation due to some individuals were easier to observe than others, what could lead to pseudoreplication. After this initial observation, we looked at the next one based on the proximity of another individual foraging or feeding. We than avoided collecting data from the same individual in the same day.

Identification of capuchin monkeys was based on individual facial characteristics and corporal attributes according to Izawa (1980). Characteristics such as body size, fur color, scars, tail shape, head shape, and face shape were some of the traces used for individual identification. The individuals were separated into infants, juveniles (I, II and III) and adults.

Observations were recorded using a DSLR camera, Canon Eos Rebel SL3, along with a telephoto lens Canon Zoom Lens EF-S 55-250mm 1:4-5.6 IS II, and videos were screened with the BORIS software (Friard & Gamba, 2016). For each sampling point, we recorded the individual's sex-age class (adult male, adult female or juvenile), and counted the positional behavior and positional behavior class performed (suspensory posture, non-suspensory posture, quadrupedal cursorial locomotion, locomotion with limbs in tension, climbing activities, bipedalism, leaping and landing), area (i.e. natural or urban) and substrate (i.e. arboreal, building, or terrestrial) in which the individual was currently engaged.

Analyses

To access the association between the occurrence of positional behavior classes (suspensory posture, non-suspensory posture, quadrupedal cursorial locomotion, locomotion with limbs in tension, climbing activities, bipedalism, leaping and landing) and areas (i.e. natural and urban), substrates (i.e. arboreal, building and terrestrial), and sex-age classes (i.e. adult male, adult female and juveniles), and, we conducted three generalized linear models (GLM) with binomial distribution.

The occurrence of a positional behavior class was used as a binomial response variable in all models, whereas sex-age class, area, and substrate were used as explanatory categorical variables. In each model, we used only one explanatory variable. Due to zero-inflation in our dataset, we chose to use a complement log-log (cloglog) link function. Statistical analyses were performed in software R (R Core Team, 2023).

Results

In the first observation period, 34 positional behaviors were recorded, and grouped into the following behavioral categories: suspensory posture, non-suspensory posture, quadrupedal cursorial locomotion, locomotion with limbs in tension, climbing activities, bipedalism, leaping, and landing (Supplementary material S1). During the second observation period, we sampled 200, two-minute focals, totaling six hours and 40 minutes, and 2,022 observed events.

Anthropogenic area effect on Positional Behavior

Area (Natural or Urban) significantly affected positional behavior classes displayed by individuals except for non-suspensory postures, and suspensory postures. Climbing activities (Urban: probability = 13%; RR = 0.15; $p < 0.001$; Natural: probability = 11%; RR = 0.12; $p < 0.001$), leaping (Urban: probability = 0.4%; RR = 0.04; $p < 0.001$; Natural: probability = 0.2%; RR = 0.02; $p < 0.001$) and quadrupedal cursorial locomotion (Urban: probability = 35%; RR = 0.54; $p < 0.001$; Natural: probability = 28%; RR = 0.39; $p < 0.001$) were more likely to occur in urban spaces compared to the natural environment (Supplementary material S2 – Table S1). In natural areas, bipedalism (Urban: probability = 0.1%; RR = 0.01; $p < 0.001$; Natural: probability = 0.2%; RR = 0.02; $p < 0.001$) and locomotion with limbs in tension (Urban: probability = 0.6%; RR = 0.07; $p < 0.001$; Natural: probability = 10%; RR = 0.11; $p < 0.001$) were more likely to be observed. We can’t compare suspensory postures (Urban: probability =

NA; RR = NA; p = NA; Natural: probability = 65%; RR = 1.87; $p < 0.001$) (Fig. 3) according to the area because we could not estimate the probability of this behavior in urban area.

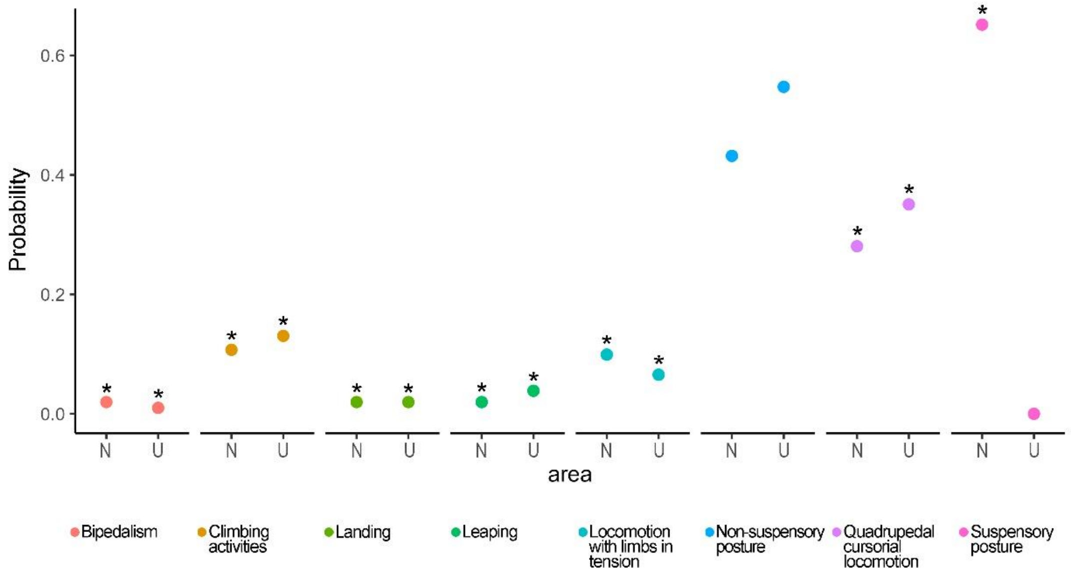

Figure 3. Probability of *Sapajus nigritus* to engage in behavior classes in urban and natural areas, in the campus of the State University of Londrina (UEL), State of Paraná, southern Brazil. N, natural; U, urban; *, significant probability $p < 0.05$.

Substrate effect on Positional Behavior

Arboreal, terrestrial, and building substrates significantly affected the likelihood of occurrence of non-suspensory postures and quadrupedal cursorial locomotion (Fig. 4; Supplementary material S2, Table S2). Non-suspensory postures are more likely to occur on terrestrial substrate (Probability = 97%; RR = 34.47; $p < 0.001$) compared to building substrate (Probability = 93%; RR = 13.08; $p < 0.001$) and arboreal substrate (Probability = 87%; RR = 6.53; $p < 0.001$). Quadrupedal cursorial locomotion was more likely to occur on the terrestrial substrate (Probability = 90%; RR = 8.45; $p < 0.001$) compared to the building (Probability = 79%; RR = 3.99 $p = 0.013$) and arboreal (Probability = 79%; RR = 3.80; $p = 0.002$) substrates. Suspensory posture was only affected by two substrates, arboreal (Probability = 98%; RR =

43.29; p < 0.001) and built (Probability = 93%; RR=13.08; p < 0.001). In this case, given the nature of suspensory behavior, terrestrial substrate was not relevant.

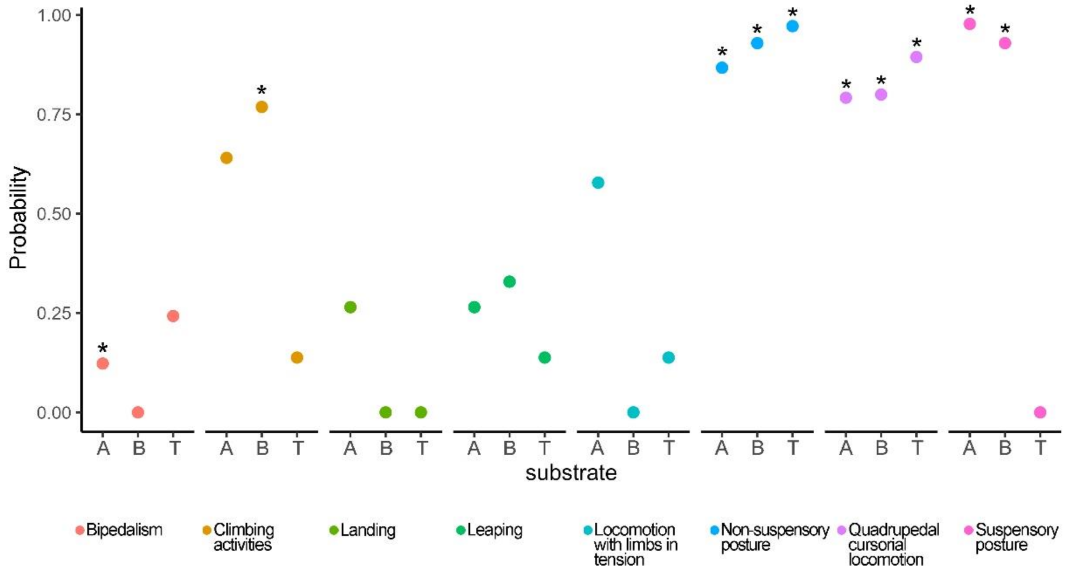

Figure 4. Probability *Sapajus nigritus* to engage in behavior classes in arboreal, built and terrestrial substrates, in the campus of the State University of Londrina (UEL), State of Paraná, southern Brazil. A, Arboreal; B, Built; T, Terrestrial; *, significant probability p < 0.05.

Sex-Age Class effect on Positional Behavior

Sex-age classes, especially juveniles and adult females, influenced most of the behaviors (p < 0.05), except for non-suspensory and suspensory postures. However, there was no greater variation in the model predictions between classes in each behavior. Juvenile were the only class that exhibit bipedalism (Probability = 0.3%; RR = 0.03; p < 0.001), and quadrupedal cursorial locomotion was only significative for juveniles (Probability = 28%; RR = 0.39; p = 0.004). The females were more likely to display climbing and landing behaviors (Climbing: Probability = 13%; RR= 0.15; p <0.001 | Landing: Probability = 0.3%; RR = 0.03; p < 0.001) followed by juveniles (Climbing: Probability = 13%; RR = 0.15; p <0.001 | Landing:

Probability = 0.2%; RR = 0.02; $p < 0.001$), with slightly difference between them. The three sex-age-classes only influenced: leaping with adult males (Probability = 0.5%; RR = 0.05; p = 0.005) showing slightly difference when compared to juveniles (Probability = 0.3%; RR = 0.03; $p < 0.001$) and adult females (Probability = 0.2%; RR = 0.02; $p < 0.001$) We found that juveniles (Probability = 0.9%; RR = 0.10; $p < 0.001$) were more likely to display locomotion with limbs in tension than adult females (Probability = 0.6%; RR = 0.07; $p < 0.001$) and adult males (Probability = 0.5%; RR = 0.05; p = 0.004) (Fig. 5; Supplementary material S2 – Table S3).

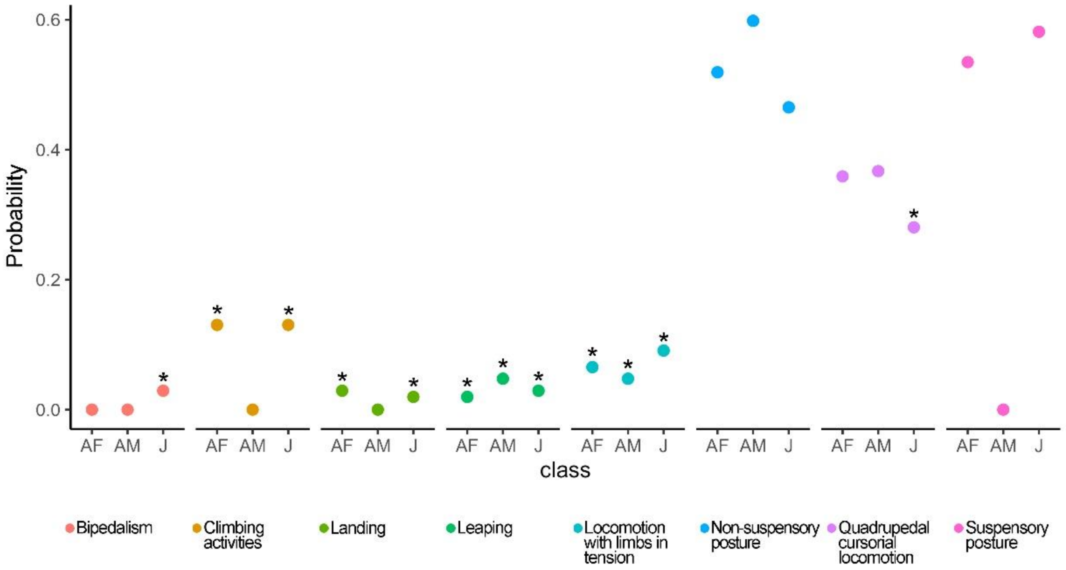

Figure 5. Probability of *Sapajus nigritus* sex-age classes to engage in positional behavior classes, in the campus of the State University of Londrina (UEL), State of Paraná, southern Brazil. AF, adult female; AM, adult male; J, juvenile; *, significant probability $p < 0.05$.

Discussion

Positional behavior in areas and substrates

The first hypothesis, related to more suspensory behaviors in urban areas, cannot be evaluated, because it was not possible to estimate the probability of the suspensive behavior in the urban areas. However, we find others interesting results, as the highest probability for suspending behaviors to occur on arboreal substrates, and the higher probability for quadrupedal cursorial locomotion to occur in urban area.

The suspensory behavior was the most performed in this study, which contrasts to other studies conducted in natural areas, where there was a lower rate of suspension (Wright et al., 2019; Youlatos, 1998). This contrast may be related to the presence of buildings, as in our study area, the arboreal substrate is representative of both the urban areas and the natural areas in campus.

Regarding to built substrates, capuchin monkeys probability to engage in non-suspensory and suspensory postures was very similar. It is possible that these animals are habituated to anthropized areas, indicating that this environment is not necessarily a determining factor in the performance of these behaviors.

The presence of capuchin and visitation rates to urban sites have been related to the abundance of anthropogenic food (Gutierres et al., 2023) provided both directly and indirectly (i.e. trash cans and university’s livestock feed) by humans (Patterson, et al., 2018). To access these anthropogenic food sources in urban areas, individuals often have to descend from suspensory postures in arboreal and adopt quadrupedal cursorial locomotion in terrestrial substrate. Therefore, the motivation to search/find and forage on trash cans could explain the difference in the use of quadrupedal cursorial locomotion.

The preference for quadrupedal cursorial locomotion may also be associated with a low sense of danger related to the urban environment and humans (Míkula et al., 2018). Capuchins that live on campus are habituated to the presence of humans and the urbanized area (França et al., 2023) and due to their great behavioral plasticity, they could be determining strategies to interact with anthropized environments and humans to obtain food (Lousa et al., 2022). When habituated to humans and acquiring food in anthropized environments, capuchin monkeys tend to develop positive interaction with humans (Sabbatini et al., 2006; Suzin et al., 2017). A low sense of danger may be associated with a higher probability of quadrupedal locomotor behaviors in urban areas due to the exploitation of food supply and feeding opportunities in these urban locations (by people and indirect food) are closer to the terrestrial substrate and spatially dispersed.

Positional behavior in regarding sex-age classes

Our second hypotheses were partially supported, our prediction (a) is partially accepted because adult male slightly leaps more than juveniles, but juveniles was the only class that exhibit bipedalism and has more probability to do the locomotion with limbs in tension. These differences can be related to the flexibility training reported by Fontaine (1994), or just because juveniles are naturally exploiting more the habitat, so is expected to their demonstrated a more diverse positional repertoire (Bezanson, 2006) with that a more diverse locomotor behavior.

Our prediction (b) related to suspensory behaviors in classes, wasn't supported. The differences in the probabilities of suspensory behavior are not significantly different in the sex-age classes. Overall, the probability of engaging in specific position behaviors was more similar between adult female and juveniles than adult males. Capuchin monkey females and males have distinct spatial use, specifically regarding to substrate usage; this difference in substrate occupation is possibly related to a differential notion of danger between the sexes (Fragaszy, 1990). Differences in substrate use between adults were also associated to niche differences and competition avoidance, when male and female capuchins would opt for different substrates (Williamson et al., 2021). This similarity between the sexes may be related to a possible low sense of danger among all adult individuals, leading them to explore all substrates in search of anthropogenic food resources.

Conclusion

Our research contributed with the knowledge of capuchin's positional behavior by adding the first positional behavior description of *Sapajus nigritus*, including the influence of urban areas across *Sapajus nigritus* positional behavior, and their utilization of urban space in contrast with natural areas (ou spaces).

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References

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3), 227–266. https://brill.com/view/journals/beh/49/3-4/article-p227_3.xml

Avis, V. (1962). Brachiation: The Crucial Issue for Man's Ancestry. *Southwestern Journal of Anthropology*, *18*(2), 119–148. https://doi.org/10.1086/soutjanth.18.2.3629013

Back, J., Suzin, A., & Aguiar, L. (2019). Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (Primates: Cebidae). *Zoologia*, *36*, 1–10. https://doi.org/10.3897/zoologia.36.e30845

Bates, et al. 2014.**Fitting linear mixed-effects models using lme4**. arXiv preprint arXiv:1406.5823.

Bergeson, D. J. (1998). Patterns of Suspensory Feeding in *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. *Springer EBooks*, 45–60. https://doi.org/10.1007/978-1-4899-0092-0_3

Bezanson, M. (2009). Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*. *American Journal of Physical Anthropology*, *140*(3), 508–517. https://doi.org/10.1002/ajpa.21099

Bezanson, M. (2017). Primate Positional Behavior Development and Evolution. *Annual Reviews*, *46*(1), 279–298. https://doi.org/10.1146/annurev-anthro-102116-041503

Bezanson, M. F. (2006). Leap, Bridge, or Ride? Ontogenetic Influences on Positional Behavior in *Cebus* and *Alouatta*. *Kluwer Academic Publishers EBooks*, 333–348. https://doi.org/10.1007/0-387-25872-8_16

Bezanson, M., & Morbeck, M. E. (2013). Future Adults or Old Children? Integrating Life History Frameworks for Understanding Primate Positional Patterns. In *Building Babies* (pp. 435–458). Springer New York, NY.

Canale, G. R., Kierulff, M. C. M., & Chivers, D. J. (2013). A Critically Endangered Capuchin Monkey (*Sapajus xanthosternos*) Living in a Highly Fragmented Hotspot. *Primates in Fragments*, 299–311. https://doi.org/10.1007/978-1-4614-8839-2_20

Cant, J. G. H. (1986). Locomotion and Feeding Postures of Spider and Howling Monkeys: Field Study and Evolutionary Interpretation. *Folia Primatologica*, *46*(1), 1–14. https://doi.org/10.1159/000156232

Cant, J. G. H. (1992). Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *American Journal of Physical Anthropology*, *88*(3), 273–283. https://doi.org/10.1002/ajpa.1330880302

Cant, J. G. H., Youlatos, D., & Rose, M. D. (2003). Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador. *Journal of Human Evolution*, *44*(6), 685–699. https://doi.org/10.1016/s0047-2484(03)00060-5

Dagosto, M., & Gebo, D. L. (1998). Methodological Issues in Studying Positional Behavior. *Primate Locomotion*, 5–29. https://doi.org/10.1007/978-1-4899-0092-0_1

Eppley, T. M., Hoeks, S., Chapman, C. A., Ganzhorn, J. U., Hall, K., Owen, M. A., Adams, D. B., Allgas, N., Amato, K. R., Andriamahaihavana, M., Aristizabal, J. F., Baden, A. L., Balestri, M., Barnett, A. A., Bicca-Marques, J. C., Bowler, M., Boyle, S. A., Brown, M., Caillaud, D., & Calegaro-Marques, C. (2022). Factors influencing terrestriality in primates of the Americas and Madagascar. *Proceedings of the National Academy of Sciences*, *119*(42). https://doi.org/10.1073/pnas.2121105119

Fleagle, J. G., & Mittermeier, R. A. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology*, *52*(3), 301–314. https://doi.org/10.1002/ajpa.1330520302

Fontaine, R. (1990). Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. *American Journal of Physical Anthropology*, *82*(4), 485–508. https://doi.org/10.1002/ajpa.1330820409

Fontaine, R. P. (1994). Play as physical flexibility training in five ceboid primates. *Journal of Comparative Psychology*, *108*(3), 203–212. https://doi.org/10.1037/0735-7036.108.3.203

Fragaszy, D. M. (1990). Sex and age differences in the organization of behavior in wedge-capped capuchins, *Cebus olivaceus*. *Behavioral Ecology*, *1*(1), 81–94. https://doi.org/10.1093/beheco/1.1.81

Fragaszy, D. M., Elisabetta Visalberghi, & Fedigan, L. M. (2004). *The Complete Capuchin*. Cambridge University Press.

França, E. A., Pereira, F. dos S. M., Lorenzo, M. P., Lynch, J. W., Orsi, M. L., & Vidotto-Magnoni, A. P. (2023). Same-sex and immature sexual behaviour repertoire in a wild group of robust capuchin monkeys. *Folia Primatologica*, *-1*(aop), 1–17. https://doi.org/10.1163/14219980-bja10009

FRIARD, O., & GAMBA, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in ecology and evolution, 7(11), 1325-1330.

Gallo, T., Fidino, M., Gerber, B., Ahlers, A. A., Angstmann, J. L., Amaya, M., Concilio, A. L., Drake, D., Gay, D., Lehrer, E. W., Murray, M. H., Ryan, T. J., St Clair, C. C., Salsbury, C. M., Sander, H. A., Stankowich, T., Williamson, J., Belaire, J. A., Simon, K., & Magle, S. B. (2022). Mammals adjust diel activity across gradients of urbanization. *ELife*, *11*. https://doi.org/10.7554/elife.74756

Garber, P. A., & Pruetz, J. D. (1995). Positional behavior in moustached tamarin monkeys: effects of habitat on locomotor variability and locomotor stability. *Journal of Human Evolution*, *28*(5), 411–426. https://doi.org/10.1006/jhev.1995.1032

Garber, P. A., & Rehg, J. A. (1999). The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, *110*(3), 325–339. https://doi.org/10.1002/(sici)1096-8644(199911)110:3%3C325::aid-ajpa5%3E3.0.co;2-d

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gebo, D. L. (1992). Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *American Journal of Primatology*, *26*(4), 277–290. https://doi.org/10.1002/ajp.1350260405

The IUCN Red List of Threatened Species. (2023). IUCN Red List of Threatened Species; https://www.iucnredlist.org/search?taxonomies=100691&searchType=species

Johnson, S. E., & Shapiro, L. J. (1998). Positional behavior and vertebral morphology in atelines and cebines. *American Journal of Physical Anthropology*, *105*(3), 333–354.

https://doi.org/10.1002/(sici)1096-8644(199803)105:3%3C333::aid-ajpa4%3E3.0.co;2-s

Laird, M. F., Punjani, Z., Oshay, R. R., Wright, B. W., Fogaça, M. D., Casteren, A., Izar, P., Visalberghi, E., Fragazy, D., Strait, D. S., Ross, C. F., & Wright, K. A. (2022). Feeding postural behaviors and food geometric and material properties in bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Biological Anthropology*. https://doi.org/10.1002/ajpa.24501

Lawler, R. R., Ford, S. M., Wright, P. C., & Easley, S. P. (2006). The Locomotor Behavior of *Callicebus brunneus* and *Callicebus torquatus*. *Folia Primatologica*, *77*(3), 228–239. https://doi.org/10.1159/000091232.

Leite, J. R. (2012). *Corredores ecológicos na Reserva da Biosfera do Cinturão Verde de São Paulo: a possibilidade e conflitos.* [Doctoral Dissertation].

Lorenzo, M. P. (2018). *Comportamento e Ecologia de uma População de Macacos-prego (Sapajus nigritus Goldfuss, 1809) em um Fragmento Florestal Inserido em Área Urbana no Município de Londrina, Paraná, Brasil* [Unpublished Master’s degree dissertation].

Lousa, T. C., de Grande, T. O., & Mendes, F. D. C. (2022). Time budget and foraging strategies of two provisioned groups of tufted capuchin monkeys, *Sapajus libidinosus*, in a small, seasonal urban forest fragment. *Primates*, *63*(4), 387–395. https://doi.org/10.1007/s10329-022-00993-3

Lüdecke D (2023). sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.15, https://CRAN.R-project.org/package=sjPlot

Ludwig, G., de Melo, F. R., Martins, W. P., Lynch Alfaro, J. W., Alonso, A. C., dos Santos, M. C., & Rímoli, J. (2015). *Sapajus nigritus*: Ludwig, G., de Melo, F.R., Martins, W.P., Miranda, J.M.D., Lynch Alfaro, J.W., Alonso, A.C., dos Santos, M.C. &

Rímoli, J. *IUCN Red List of Threatened Species*. https://doi.org/10.2305/iucn.uk.2021-1.rlts.t136717a192593806.en

Lynch Alfaro, J. W., Izar, P., & Ferreira, R. G. (2014). Capuchin monkey research priorities and urgent issues. *American Journal of Primatology*, *76*(8), 705–720. https://doi.org/10.1002/ajp.22269

Martin, P., & Bateson, P. (2007). *Measuring Behaviour*. Cambridge University Press.

Martins, W. P., Izar, P., Santos, W., Henrique, F., & Alfaro, J. L. (2022). Diet, activity patterns, and home range use in forest and cultivated areas for one wild group of endangered crested capuchin monkeys (*Sapajus robustus*) in Reserva Natural Vale, Espírito Santo, Brazil. *American Journal of Primatology*, *84*(8). https://doi.org/10.1002/ajp.23413

Mikula, P., Šaffa, G., Nelson, E., & Tryjanowski, P. (2018). Risk perception of vervet monkeys *Chlorocebus pygerythrus* to humans in urban and rural environments. *Behavioural Processes*, *147*, 21–27. https://doi.org/10.1016/j.beproc.2017.12.011

Morbeck, M. E. (1977). Positional behavior, selective use of habitat substrate and associated non-positional behavior in free-ranging *Colobus guereza* (Rüppel, 1835). *Primates, 18*(1), 35–58. https://doi.org/10.1007/bf02382952

Mota, F. M. M., Leite, M. R., & Martins, W. P. (2018). Fragmentation dynamics and loss of area of potential occupancy within the distribution limits of the endangered crested capuchin monkey (*Sapajus robustus*). *American Journal of Primatology, 80*(9), e22906. https://doi.org/10.1002/ajp.22906

Patterson, L., Kalle, R., & Downs, C. (2018). Factors affecting presence of vervet monkey troops in a suburban matrix in KwaZulu-Natal, South Africa. *Landscape and Urban Planning*, *169*, 220–228. https://doi.org/10.1016/j.landurbplan.2017.09.016

Patterson, L., Kalle, R., & Downs, C. T. (2019). Living in the suburbs: Space use by vervet monkeys (*Chlorocebus pygerythrus*) in an eco-estate, South Africa. *African Journal of Ecology*, *57*(4), 539–551. https://doi.org/10.1111/aje.12629

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenberger, A. L. (1992). Evolution of feeding niches in new world monkeys. *American Journal of Physical Anthropology*, *88*(4), 525–562. https://doi.org/10.1002/ajpa.1330880408

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Rudnick, D. A., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C. W., Gerber, L. R., Hartter, J., Jenness, J. S., Kintsch, J., Merenlender, A. M., Perkl, R. M., Preziosi, D. V., & Trombulak, S. C. (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Ecological Society of America*, *16*, 1–23.

Sabbatini, G., Stammati, M., Tavares, M. C. H., Giuliani, M. V., & Visalberghi, E. (2006). Interactions between humans and capuchin monkeys (*Cebus libidinosus*) in the Parque Nacional de Brasília, Brazil. *Applied Animal Behaviour Science*, *97*(2-4), 272–283. https://doi.org/10.1016/j.applanim.2005.07.002

Suzin, A., Back, J. P., Garey, M. V., & Aguiar, L. M. (2017). The Relationship Between Humans and Capuchins (*Sapajus* sp.) in an Urban Green Area in Brazil. *International Journal of Primatology*, *38*(6), 1058–1071. https://doi.org/10.1007/s10764-017-9996-3

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Available from: https://ggplot2.tidyverse.org.

Williamson, R. E., Webb, S. E., Dubreuil, C., Lopez, R., Cheves Hernandez, S., Fedigan, L. M., & Melin, A. D. (2021). Sharing spaces: niche differentiation in diet and substrate use among wild capuchin monkeys. *Animal Behaviour*, *179*, 317–338. https://doi.org/10.1016/j.anbehav.2021.06.002

Wright, K. A. (2007). The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. *American Journal of Primatology*, *69*(7), 736–756. https://doi.org/10.1002/ajp.20391

Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., & Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, *81*(12). https://doi.org/10.1002/ajp.23067

Youlatos, D. (1998). Positional behavior of two sympatric guianan capuchin monkeys, the brown capuchin (*Cebus apella)* and the wedge-capped capuchin (*Cebus olivaceus*). *Mammalia*, *62*(3). https://doi.org/10.1515/mamm.1998.62.3.351

Youlatos, D. (1999). Comparative locomotion of six sympatric primates in Ecuador. *Annales Des Sciences Naturelles - Zoologie et Biologie Animale*, *20*(4), 161–168. https://doi.org/10.1016/s0003-4339(00)88884-x

Youlatos, D. (2002). Positional behavior of black spider monkeys (*Ateles paniscus*) in french guiana. *International Journal of Primatology*, *23*(5), 1071–1093. https://doi.org/10.1023/a:1019602116805

Youlatos, D. (2008). Locomotion and positional behavior of spider monkeys. *Spider Monkeys*, 185–219. https://doi.org/10.1017/cbo9780511721915.007

Supplementary material S1: Positional behavior ethogram of *Sapajus nigritus.*

Table 1. Positional behavior ethogram of black-horned capuchin monkey (*Sapajus* nigritus): Categories and behaviors observed during foraging and feeding.

Category	Positional Behavior	Description	Figure
SUSPENSORY POSTURES	1. Suspension by both hindlimbs.	The individual is not on the terrestrial substrate and remains suspended by its hind limbs.	Fig. 1
	2. Suspension by a single hindlimb.	Similar to the "hanging with both hind limbs" posture, but the individual maintains support on only one of the hind limbs.	Fig. 2
	3. Suspension by both hindlimbs and a single forelimb.	The individual holds itself in suspension with its hind limbs and only one forelimb, in the picture we have an individual holding this posture while carrying food in one forelimb.	Fig. 3
	4. Suspension by all four limbs.	The individual remains suspended on both fore and hind limbs and can use the tail for support.	Fig. 4
	5. Suspension by both hindlimbs.	The individual remains suspended using only their forelimbs.	Fig. 5
	6. Suspension by a single hindlimb.	The individual remains suspended with only one forelimb.	Fig. 6
	7. Suspension by one forelimb and one hindlimb.	The individual hangs from one forelimb and one hindlimb and can use its tail for support.	Fig. 7
	8. Suspension by the prehensile tail.	The individual remains suspended using only its tail.	Fig. 8
NON-SUSPENSORY POSTURES	1. Bipedal standing orthograde.	The individual stands bipedal with the body vertically upright on the substrate.	Fig. 9
	2.Bipedal standing pronograde.	The individual stands bipedal with its body diagonal or horizontal to the substrate.	Fig. 10
	3.Tripedal standing.	The individual stands with three limbs for support in contact with the substrate.	Fig. 11

	4.Quadrupedal standing.	The individual stands with all four limbs as a support in contact with the substrate.	Fig. 12
	5.Inverted bipedalism.	Inverted bipedalism is characterized by a posture in which the animal holds its prehensile tail under tension while the hindlimbs are under compression, with the head facing the ground.	Fig. 13
	6.Vertical clinging.	When holding itself upright, the animal keeps its body attached to a vertical support, flexes all its limbs, and keeps its hands and feet in contact with the substrate.	Fig. 14
	7.Sitting.	The animal distributes its weight over the substrate, maintaining a prone to fully orthograde posture. Other limbs can be seen providing support.	Fig. 15
	8.Orthograde lay back posture.	The animal lies down keeping its back in contact with the substrate.	Fig. 16
QUADRUPEDAL CURSORIAL LOCOMOTION	1.Quadrupedal walking.	The quadruped gait is a symmetrical locomotion with diagonal and lateral sequences in a pronograde quadrupedal locomotion that varies from slow to moderately fast.	Fig. 17
	2.Quadrupedal running.	Quadrupedal running is characterized by being a faster movement compared to quadrupedal walking.	Fig. 17
	3.Tripedal walking.	Tripedal walking is similar to quadruped walking and running, but the animal uses one forelimb to carry an object.	Fig. 18
	4.Quadrupedal bounding.	The quadrupedal bounding gait is characterized by asymmetrical quadrupedal locomotion that varies from moderate to fast, the forelimbs appear to move forward being followed concomitantly by the movements of the hind limbs, generating the jumps during locomotion and each pair of limbs appears to encounter the substrate at the same time.	Fig. 19

	5.Galloping.	Similar to the quadrupedal bounding gait, the gallop is characterized by a fast, asymmetrical stride in which the right and left limbs of each pair (fore and hind) are slightly out of sync.	Fig. 20
LOCOMOTION EMPHASIZING USE OF THE LIMBS IN TENSION	1.Pronograde bridging.	This posture is characterized by being a way of passing between discontinuous arboreal spaces. It begins with an incomplete jump in which the animal grasps the support and pulls its body towards it. The animal remains stretched between the supports with all its limbs under tension.	Fig. 21
CLIMBING ACTIVITIES	1.Quadrupedal climbing.	It is characterized by a vertical quadrupedal ascent with an apparently symmetrical stride. The forelimbs move toward the supports above the animal's head and pull it upward, while the hindlimbs push it upward. This form of climbing may have variations, such as a tripedal climb while holding an object.	Fig. 22
	2.Shinnying.	Vertical ascent in which the hind limbs act as propulsion and the forelimbs act as a pivot, holding on to the support.	Fig. 23
	3. Rear-first quadrupedal descent.	Symmetrical quadruped descent with tail and hindlimbs descending first.	Fig. 24
	4.Head-first quadrupedal descent.	Symmetrical quadruped descent with head and forelimbs descending first.	Fig. 25
BIPEDALISM	1.Unassisted bipedal locomotion.	Bipedal locomotion without the aid of forelimbs or tail.	Fig. 26
	2.Assisted bipedal locomotion.	Bipedal locomotion in which the animal uses the movements of its forelimbs as an aid. In this case, the animal uses the object carried by its forelimbs as support.	Fig. 27
LEAPING	1.Slow quadrupedal.	The jumping motion is generated by rapid flexion and the propulsive force of hind limb extension. The jump begins in a static squatting position.	Fig. 28
	2.Bipedal take-off.	It starts from a bipedal positure where the animal flexes and	Fig. 29

		extends its hind limbs, generating a propulsive force.	
	3.Tail suspension.	Passive suspension of the tail before the fall, while the animal observes the ground, the movement occurs when the animal releases the tail support and falls onto the substrate.	Fig. 30
LANDING MODES FOR LEAPING/DROPPING	1.Quadrupedal pronograde.	It is characterized by a horizontal landing and the presence of an oblique support. In most cases, the forelimbs touch the terminal support before the hindlimbs. All limbs appear to be strongly impacted by compressive forces upon reaching the support.	Fig. 31
	2. Vertical.	It is characterized by a vertical landing and the presence of a vertical support. The hind limbs appear to touch the terminal support before the forelimbs in most cases.	Fig. 32
	3.Hindlimb-forelimb suspensory.	Landing in suspension, using both fore and hind limbs, while the tail may serve as a support.	Fig. 33

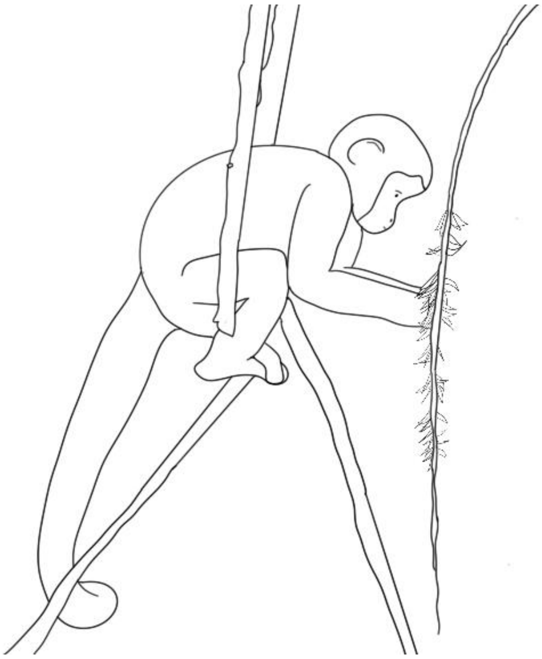

Figure 1. Suspensory Posture. Suspension by both hindlimbs.

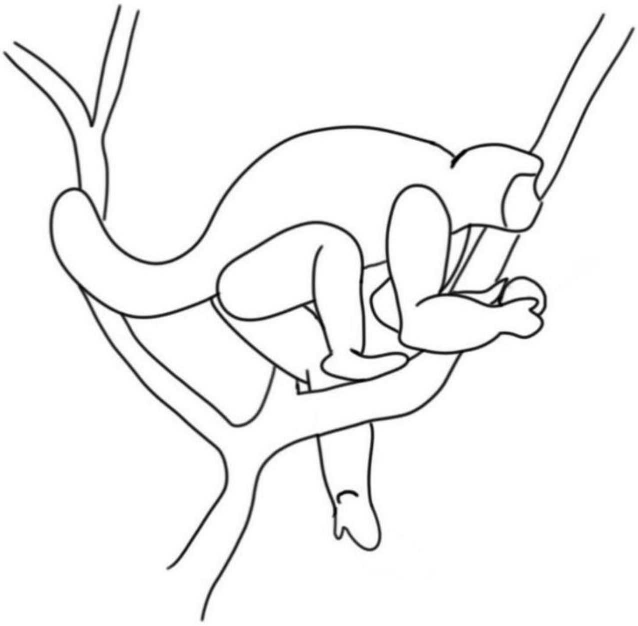

Figure 2. Suspensory posture. Suspension by a single hindlimb.

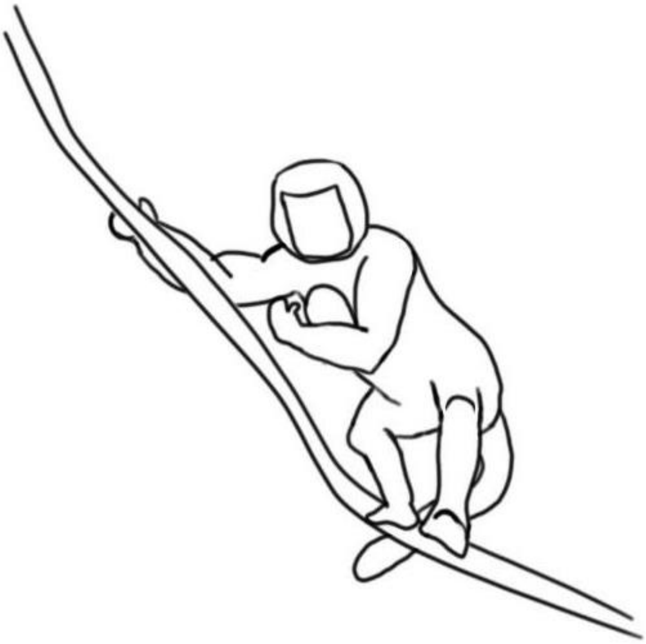

Figure 3. Suspensory posture. Suspension by both hindlimbs and a single forelimb.

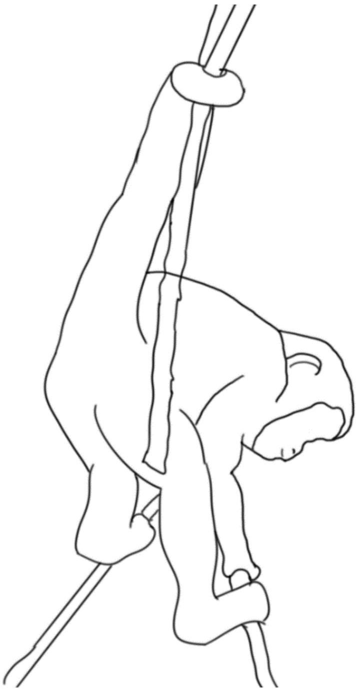

Figure 4. Suspensory posture. Suspension by all four limbs.

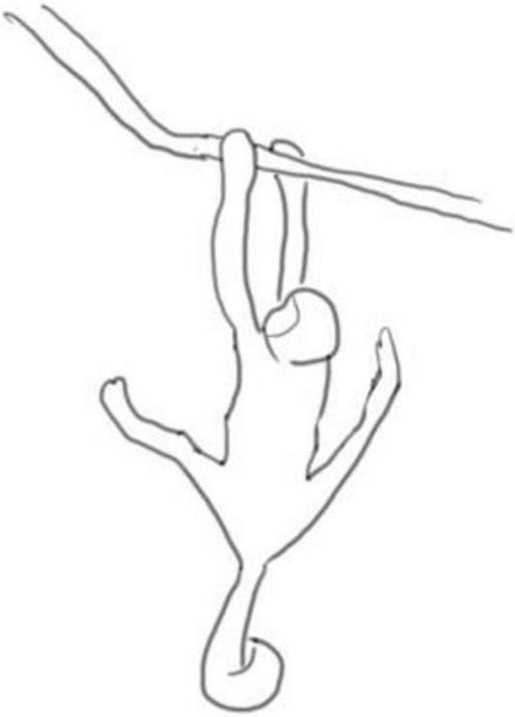

Figure 5. Suspensory posture. Suspension by both hindlimbs.

Figure 6. Suspensory posture. Suspension by a single hindlimb.

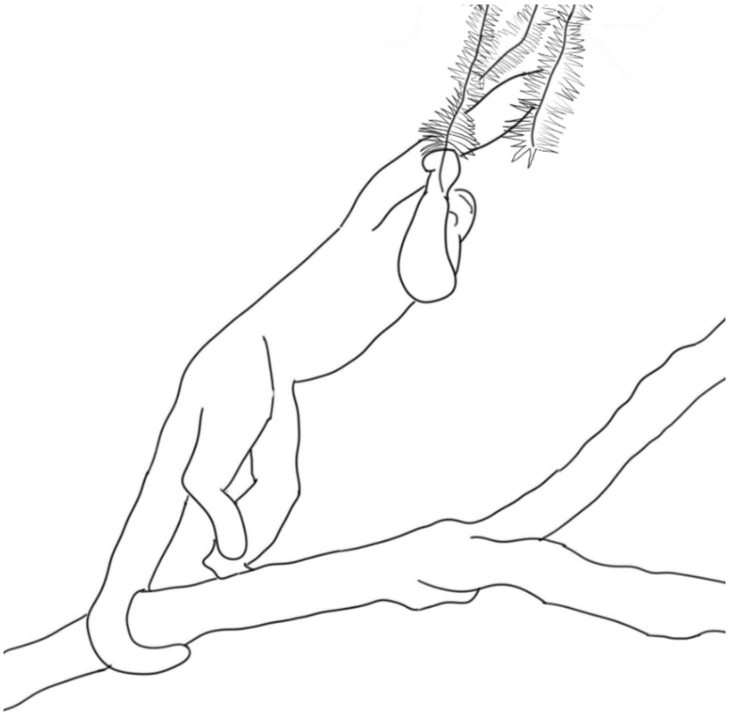

Figure 7. Suspensory posture. Suspension by one forelimb and one hindlimb.

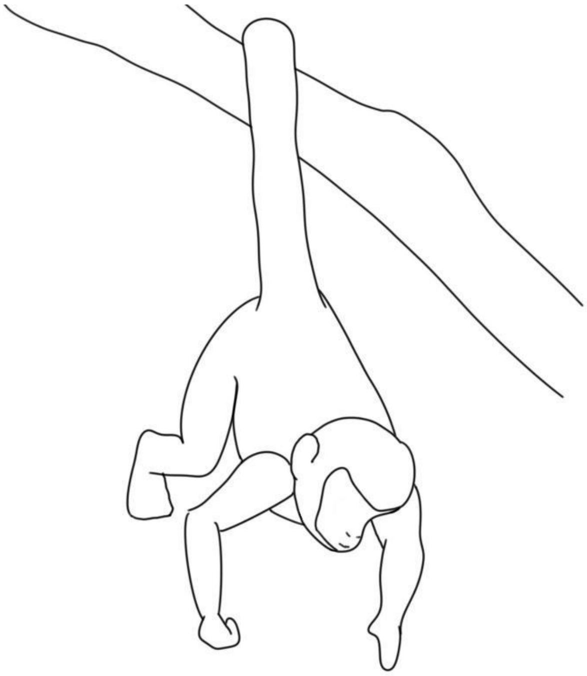

Figure 8. Suspensory posture. Suspension by the prehensile tail.

Figure 9. Non suspensory posture. Bipedal standing orthograde.

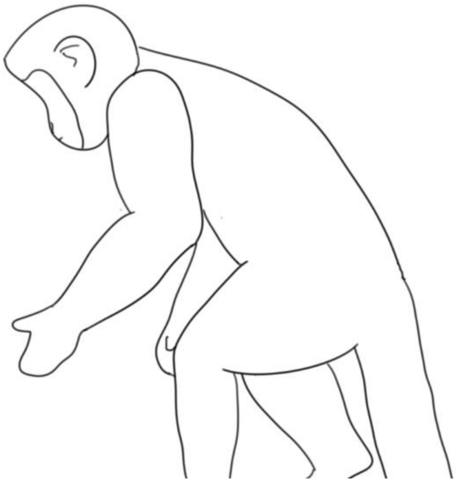

Figure 10. Non suspensory posture. Bipedal standing pronograde.

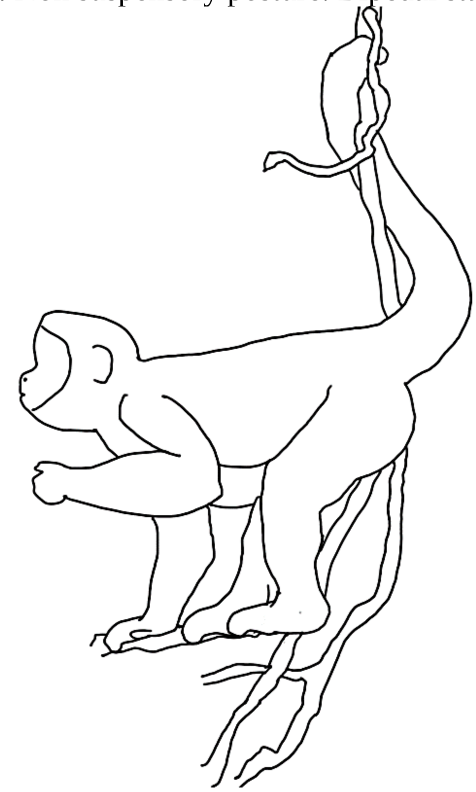

Figure 11. Non suspensory posture. Tripedal standing.

Figure 12. Non suspensory posture. Quadrupedal standing.

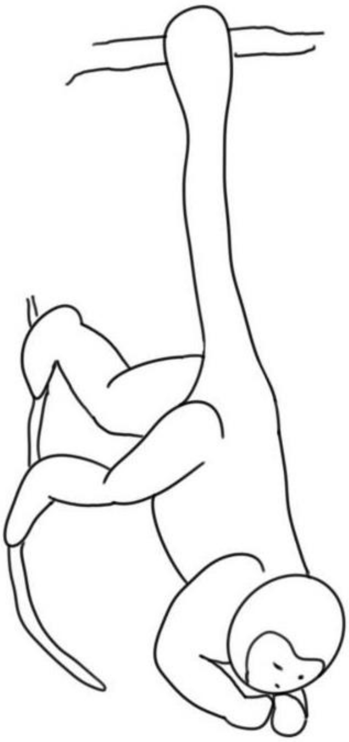

Figure 13. Non suspensory posture. Inverted bipedalism.

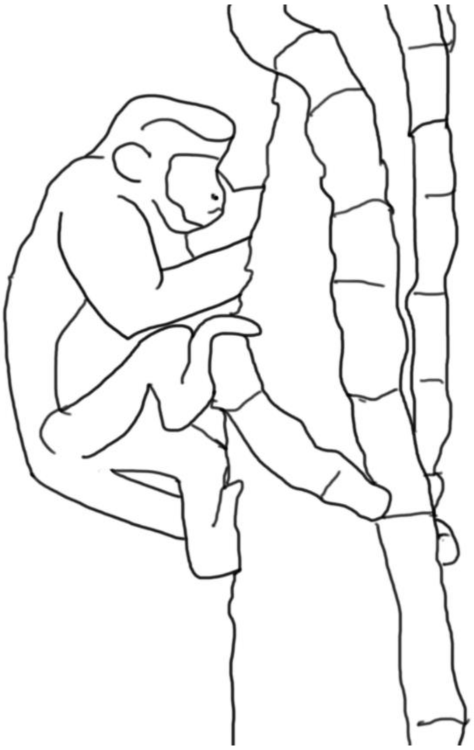

Figure 14. Non suspensory posture. Vertical clinging.

Figure 15. Non suspensory posture. Sitting.

Figure 16. Orthograde lay back posture.

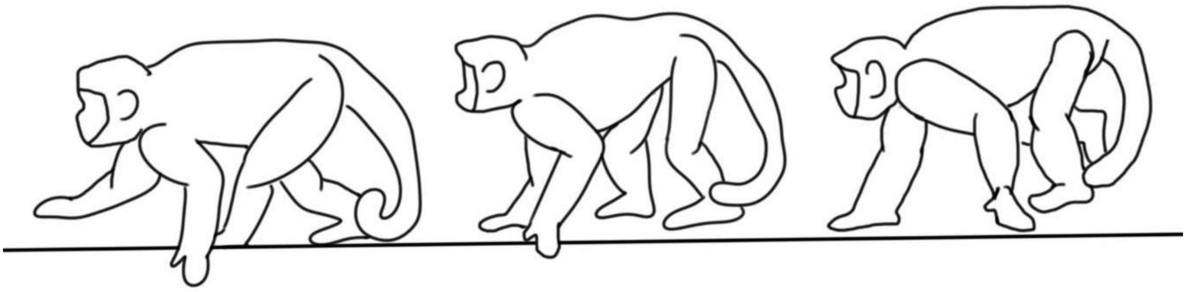

Figure 17. Quadrupedal cursorial locomotion. Quadrupedal walking/running.

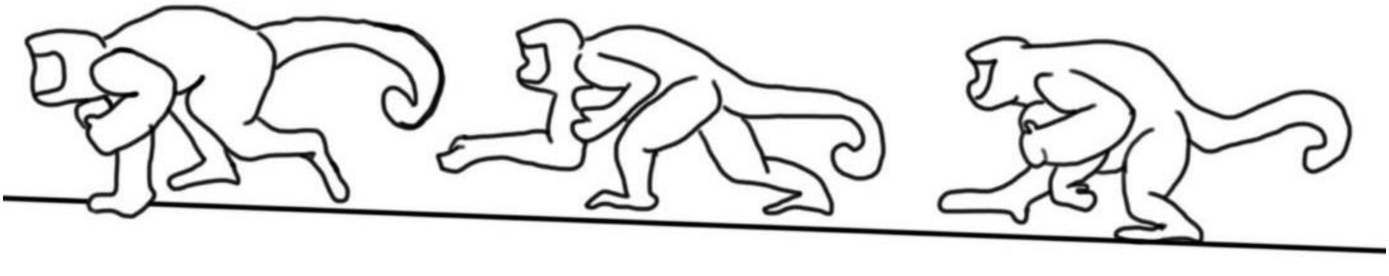

Figure 18. Quadrupedal cursorial locomotion. Tripedal walking.

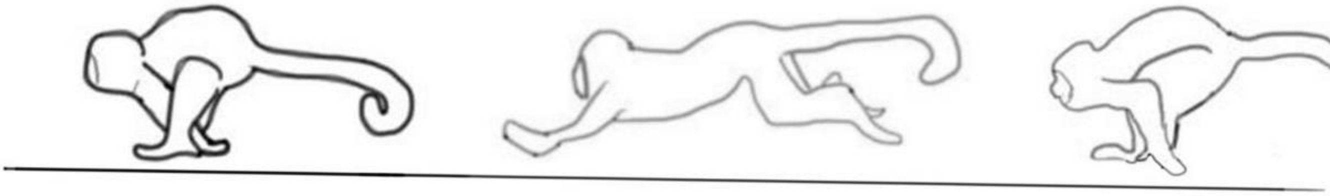

Figure 19. Quadrupedal cursorial locomotion. Quadrupedal bounding.

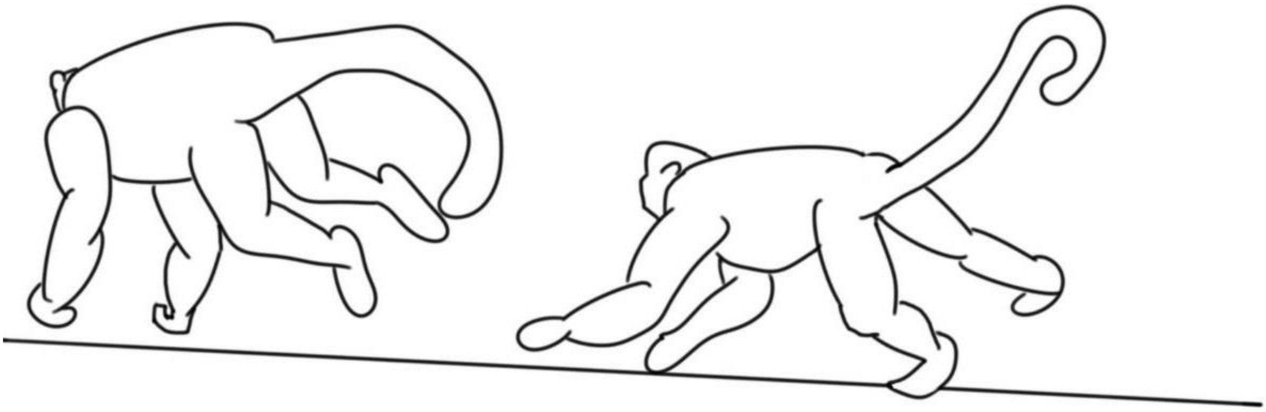

Figure 20. Quadrupedal cursorial locomotion. Galloping.

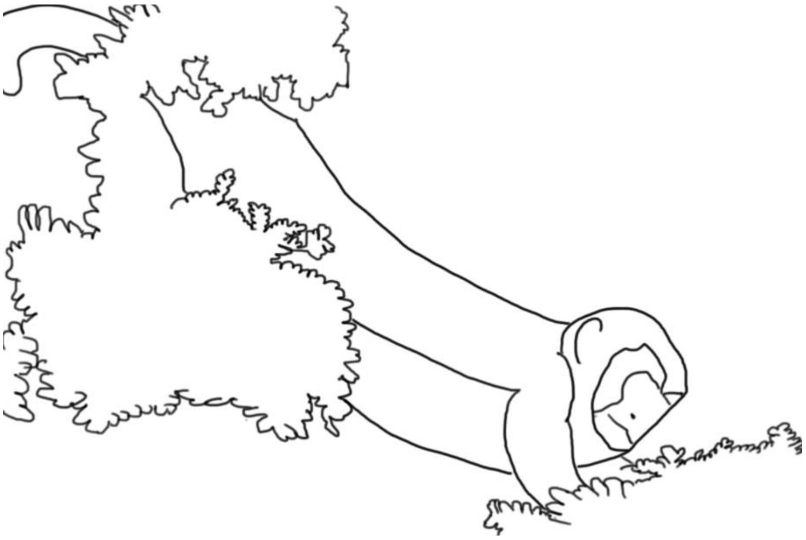

Figure 21. Locomotion emphasizing use of the limbs in tension. Pronograde bridging.

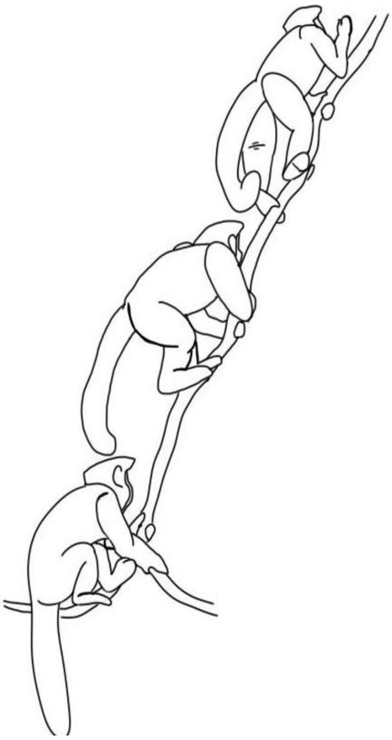

Figure 22. Climbing activities. Quadrupedal climbing.

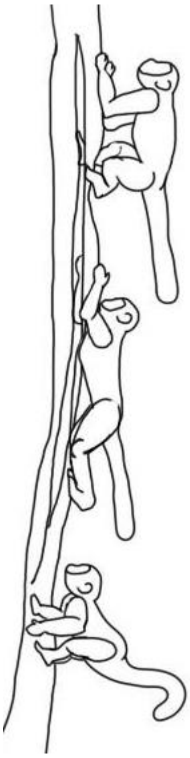

Figure 23. Climbing activities. Shinnying.

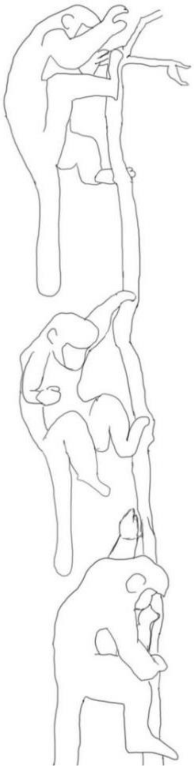

Figure 24. Climbing activities. Rear-first quadrupedal descent.

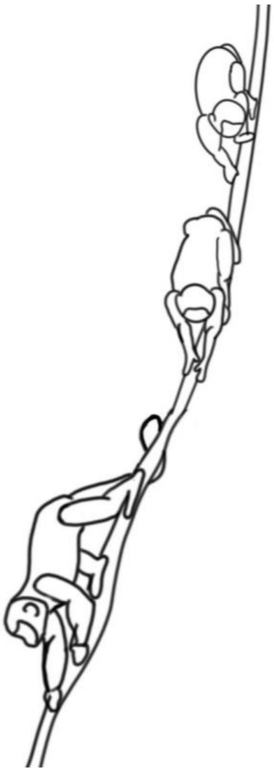

Figure 25. Climbing activities. Head-first quadrupedal descent.

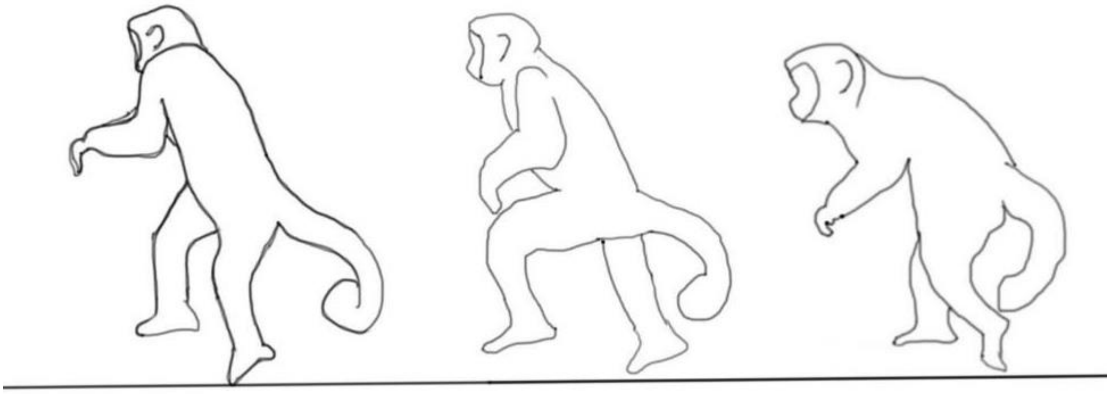

Figure 26. Bipedalism. Unassisted bipedalism locomotion.

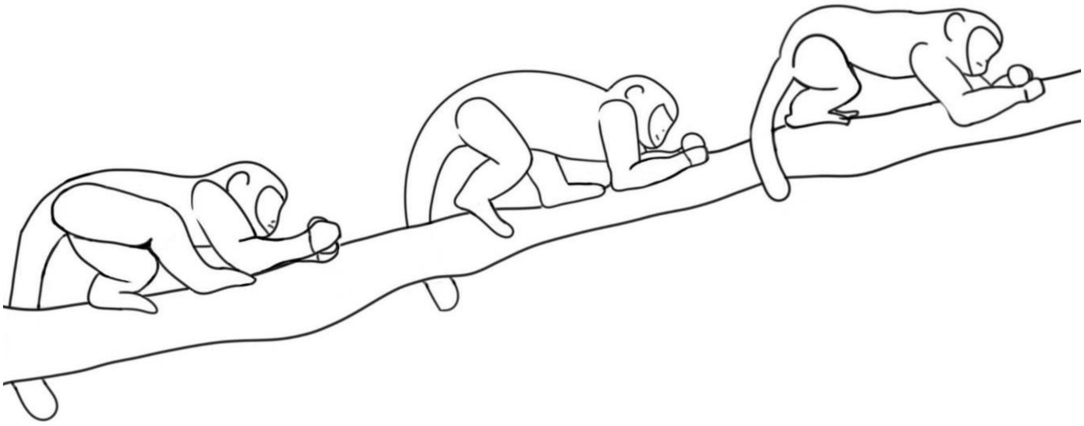

Figure 27. Bipedalism. Assisted bipedal locomotion.

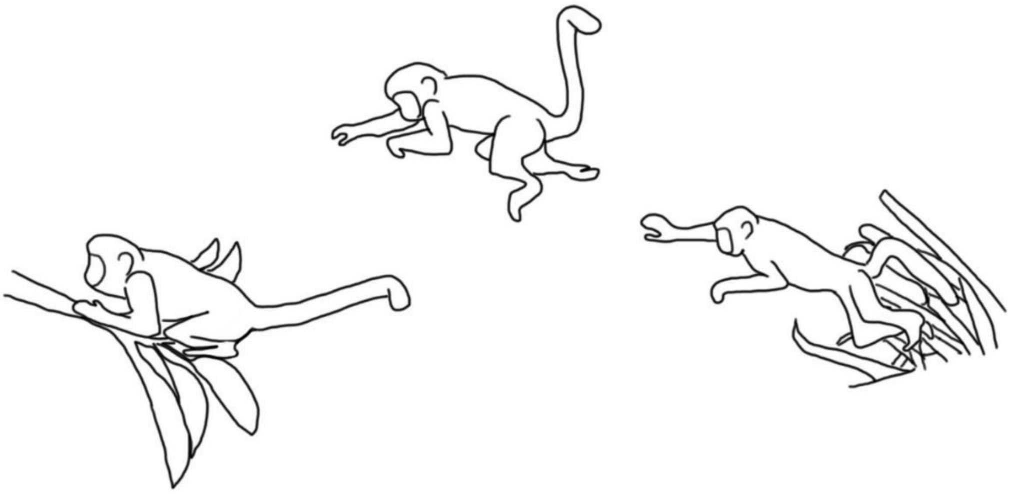

Figure 28. Leaping. Slow quadrupedal.

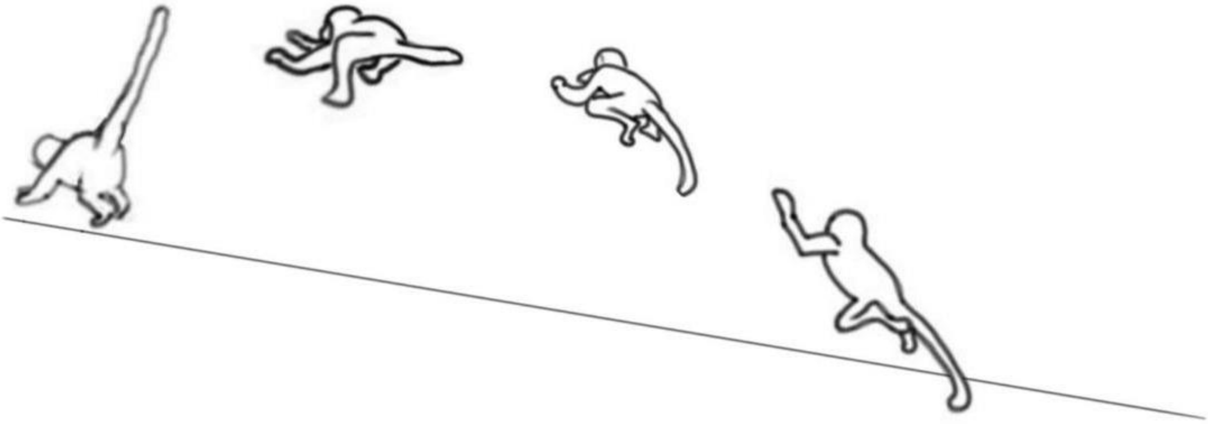

Figure 29. Leaping. Bipedal take-off.

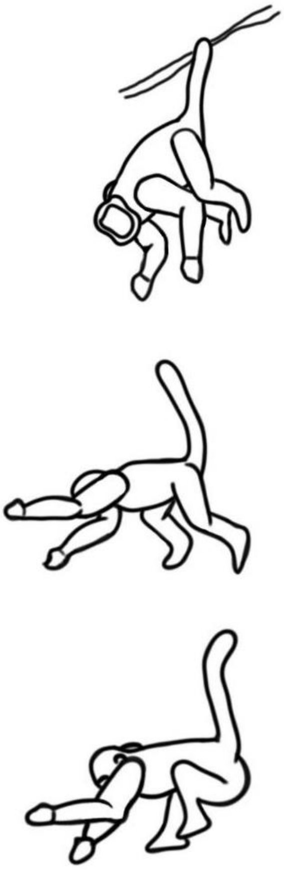

Figure 30. Leaping. Tail suspension.

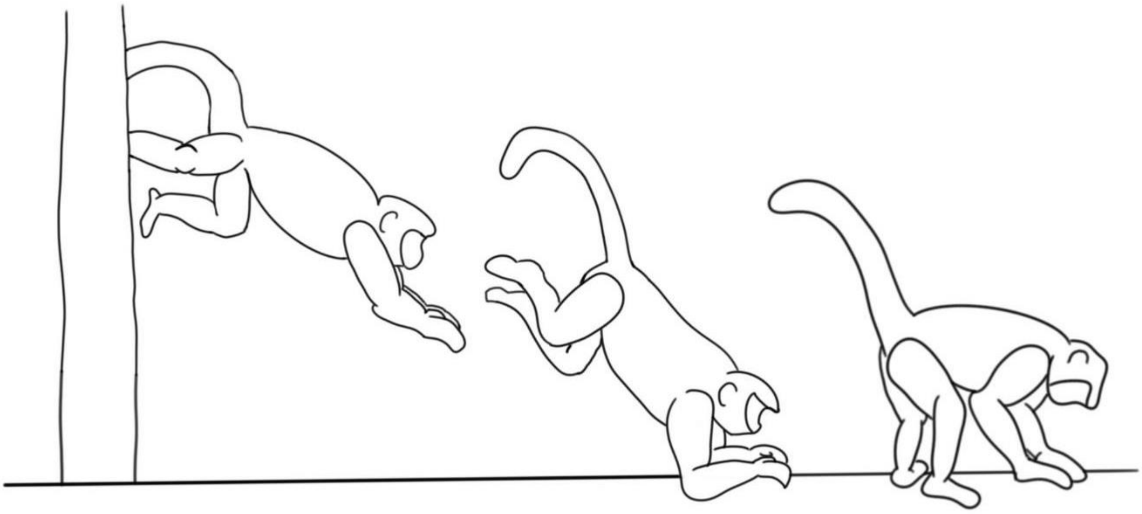

Figure 31. Landing modes for leaping/dropping. Quadrupedal pronograde.

Figure 32. Landing modes for leaping/dropping. Vertical.

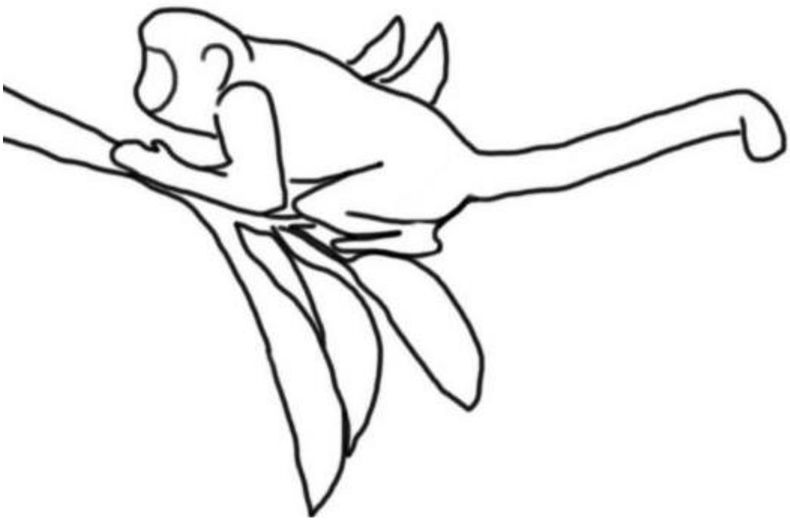

Figure 33. Landing modes for leaping/dropping. Hindlimb-forelimb suspensory.

Supplementary material S2: Probability of positional behavior of *Sapajus nigritus*.

Table S1: Probability and occurrence risk ratio estimates from generalized linear model of the relationship between behaviors and area.

Behavior	Area	Probability (%)	Ocurrence *Risk ratios*	*CI*	*p*
	(Intercept)	0,49	0,95	0,76 – 1,17	0,651
Bipedalism	Natural	0,02	0,02	0,00 – 0,07	**<0,001**
	Urban	0,01	0,01	0,00 – 0,05	**<0,001**
Climbing activities	Natural	0,11	0,12	0,06 – 0,22	**<0,001**
	Urban	0,13	0,15	0,09 – 0,24	**<0,001**
Landing	Natural	0,02	0,02	0,00 – 0,07	**<0,001**
	Urban	0,02	0,02	0,01 – 0,06	**<0,001**
Leaping	Natural	0,02	0,02	0,01 – 0,06	**<0,001**
	Urban	0,04	0,04	0,01 – 0,08	**<0,001**
Locomotion with limbs in tension	Natural	0,10	0,11	0,05 – 0,20	**<0,001**
	Urban	0,06	0,07	0,03 – 0,13	**<0,001**
Non-suspensory postures	Natural	0,43	0,76	0,53 – 1,08	0,127
	Urban	0,54	1,21	0,89 – 1,63	0,219
Quadrupedal cursorial locomotion	Natural	0,28	0,39	0,25 - 0,58	**<0,001**
	Urban	0,35	0,54	0,38 – 0,75	**<0,001**
Suspensory Postures	Natural	0,65	1,87	1,35 – 2,59	**<0.001**
	Urban	NA	NA	NA	NA

Table S2: Probability and occurrence risk ratio estimates from generalized linear model of the relationship between behaviors and substrate.

Behavior	Substrate	Probability (%)	Ocurrence *Risk ratios*	*CI*	*P*
	(Intercept)				
Bipedalism	Arboreal	0,12	0,14	0,02 – 0,62	**0,018**
	Building	0,00	0,00	0,00 -0,00	0,990
	Terrestrial	0,24	0,32	0,05 – 1,40	0,167
Climbing activities	Arboreal	0,64	1,78	0,77 – 4,82	0,210
	Building	0,77	3,32	1,04 – 10,64	**0,038**
	Terrestrial	0,14	0,16	0,01 – 0,94	0,090
Landing	Arboreal	0,26	0,36	0,10 – 1,20	0,094
	Building	0,00	0,00	0,00 – 0,00	0,990
	Terrestrial	0,00	0,00	0,00 – 0,00	0,983
Leaping	Arboreal	0,26	0,36	0,10 – 1,20	0,094
	Building	0,33	0,49	0,03 – 2,86	0,507
	Terrestrial	0,14	0,16	0,01 – 0,94	0,090
Locomotion with limbs in tension	Arboreal	0,58	1,37	0,57 – 3,77	0,508
	Building	0,00	0,00	0,00 - 0,00	0,990
	Terrestrial	0,14	0,16	0,01 - 0,94	0,090
Non-suspensory postures	Arboreal	0,87	6,53	3,08 – 16,88	**<0,001**
	Building	0,93	13,08	5,29 – 36,94	**<0,001**
	Terrestrial	0,97	34,47	15,54 – 91,96	**<0,001**
Quadrupedal cursorial locomotion	Arboreal	0,79	3,80	1,75 – 9,94	**0,002**
	Building	0,80	3,99	1,32 – 12,42	**0,013**
	Terrestrial	0,90	8,45	3,83 – 22,32	**<0,001**
Suspensory Postures	Arboreal	0,98	43,29	20,14 – 113,24	**<0,001**
	Building	0,93	13,08	5,29 – 36,94	**<0,001**
	Terrestrial	0,00	0,00	0,00	0,00

Table S3: Probability and occurrence risk ratio estimates from generalized linear model of the relationship between behaviors and sex-age classes.

Behavior	Sex-class	Probability (%)	*Ocurrence Risk ratios*	*CI*	*p*
	(Intercept)	0,49	0,97	0,52 – 1,63	0,902
Bipedalism	AF	0,00	0,00	0,00 – 0,00	0,965
	AM	0,00	0,00	0,00 – 0,00	0,983
	J	0,03	0,03	0,00 – 0,09	**<0,001**
Climbing activities	AF	0,13	0,15	0,06 – 0,33	**<0,001**
	AM	0,00	0,00	0,00 – 0,00	0,983
	J	0,13	0,15	0,07 – 0,32	**<0,001**
Landing	AF	0,03	0,03	0,01 – 0,11	**<0,001**
	AM	0,00	0,00	0,00 – 0,00	0,983
	J	0,02	0,02	0,00 – 0,06	**<0,001**
Leaping	AF	0,02	0,02	0,00 – 0,08	**<0,001**
	AM	0,05	0,05	0,00 – 0,26	**0,004**
	J	0,03	0,03	0,10 – 0,09	**<0,001**
Locomotion with limbs in tension	AF	0,06	0,07	0,02 – 0,18	<**0,001**
	AM	0,05	0,05	0,00 – 0,26	**0,004**
	J	0,09	0,10	0,04 – 0,22	**<0,001**
Non-suspensory postures	AF	0,52	1,08	0,60 – 2,11	0,803
	AM	0,60	1,49	0,69 – 3,29	0,317
	J	0,46	0,87	0,49 – 1,67	0,649
Quadrupedal cursorial locomotion	AF	0,36	0,56	0,30 – 1,11	0,081
	AM	0,37	0,58	0,23 – 1,37	0,220
	J	0,28	0,39	0,21 – 0,77	**0,004**
Suspensory Postures	AF	0,53	1,15	0,64 – 2,23	0,661
	AM	NA	NA	NA	NA
	J	0,58	1,39	0,79 – 2,66	0,2

Supplementary material S3: frequency of positional behavior of *Sapajus nigritus*.

Suspensory postures were the most performed behaviors (N = 1060, 52.423%), in which *suspension with both hind limbs* and *suspension with all four limbs* were the most frequent behavior observed in all (43.301% and 40.471%, respectively), followed by non-suspensory postures (N = 718, 35.855%), quadrupedal cursorial locomotion (N = 154, 7.616%), locomotion with limbs in tension (N = 32, 1.582%), climbing activities (N = 34, 1.681%), bipedalism (N = 4, 0.197%), leaping (N = 8, 0.395%) and landing (N = 5, 0.247%).

Juveniles exhibited higher overall frequencies in almost all categories except for non-suspensory posture and locomotion with limbs in tension that were frequently more performed among adults. Some behaviors, such as bipedalism, were exclusively observed among juveniles. Adult males had the lowest frequency in almost all categories, except in non-suspensory posture, and quadrupedal cursorial locomotion, while adult females had the highest frequency in the locomotion with limbs in tension category (Table 1).

Table 1. Frequency (%) of behaviors grouped into categories in relation to sex-age classes of *S. nigritus*, on the campus of the State University of Londrina.

Sex-age class	Adult Male	Adult Female	Juvenile
Suspensory posture	33.838	48.593	57.749
Non-suspensory posture	57.070	39.130	30.207
Quadrupedal cursorial locomotion	8.080	8.056	7.403
Locomotion with limbs in tension	0.505	2.301	1.480
Climbing activities	-	1.406	2.171
Bipedalism	-	-	0.394
Leaping	0.505	0.383	0.394
Landing	-	0.127	0.197

Positional behaviors had a greater variation in the frequency of locations and substrates with posturing, quadruped locomotion, and locomotion with limbs in tension. (Table 2).

Table 2. Frequency (%) of *S. nigritus* positional behavior in natural and urban areas and arboreal, terrestrial, built substrates of the campus of the State University of Londrina.

Location and Substrate	**Urban**	**Natural**	**Arboreal**	**Terrestrial**	**Built**
Suspensory posture	44,378	63,561	74,205	-	38,916
Non-suspensory posture	43,356	25,471	15,582	84,242	50,246
Quadrupedal cursorial locomotion	8,858	5,896	4,992	15,151	6,403
Locomotion with limbs in tension	0,936	2,712	2,420	-	-
Climbing activities	1,788	1,533	1,966	-	3,940
Bipedalism	0,170	0,235	0,121	0,404	-
Leaping	0,425	0,235	0,378	0,202	0,492
Landing	0,085	0,353	0,302	-	-

Regarding to terrestrial substrate, only non-suspensory postures, quadrupedal cursorial locomotion, bipedalism, and leaping were observed. Almost all of them, excepted bipedalism, occurred with a higher frequency in the urban environment (Table 2).

One major difference between the natural and urban locations is the presence of the substrate edified, that only occur in urban areas. Regarding that difference, the frequency of positional behavior between urban and natural areas related to the substrates are similar (Table 3).

Table 3. Frequency (%) of positional grouping behaviors of *S. nigritus* performed in urban and natural related to substrate at the campus of the State University of Londrina.

Location with Substrates	**Urban Arboreal**	**Urban Terrestrial**	**Urban Built**	**Natural Arboreal**	**Natural Terrestrial**
Suspensory posture	71,764	-	38,916	75,928	-
Non-suspensory posture	18,487	82,571	50,246	13,075	88,275
Quadrupedal cursorial locomotion	5,042	16,571	6,403	4,903	11,724
Locomotion with limbs in tension	1,848	-	-	3,120	-
Climbing activities	1,848	-	3,940	1,931	-
Bipedalism	-	0,571	-	0,297	-
Leaping	0,504	0,285	0,492	0,445	-
Landing	0,504	-	-	0,297	-

About locomotion *Running* and *Galloping* were exclusively observed among juveniles. Other behaviors that also have higher propulsive force, here and after defined as locomotor behaviors with high speed when compared to other locomotors behaviors as quadrupedal walking or tripedal walking, that were, such as quadrupedal bounding, were observed more frequently in juveniles and less in adults (Table 4).

Table 4: Frequencies (%) of quadrupedal cursorial locomotion per classes in *S. nigritus* from the campus of the State University of Londrina.

Sex-age class	**Adult Male**	**Adult Female**	**Juvenile**
Quadrupedal walking	100	94.117	87.931
Quadrupedal running	-	-	5.172
Tripedal walking	-	2.941	-
Quadrupedal bounding	-	2.941	5.172
Galloping	-	-	1.724

4. CONCLUSÕES

Nossa pesquisa contribuiu para o conhecimento do comportamento posicional de macacos-prego, acrescentando a primeira descrição do comportamento posicional de *Sapajus nigritus*, com o efeito das áreas urbanas no comportamento posicional de *Sapajus nigritus* e sua utilização de espaços urbanos em comparação com os fragmentos florestais.

5.REFERÊNCIAS

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3), 227–266. https://brill.com/view/journals/beh/49/3-4/article-p227_3.xml

Avis, V. (1962). Brachiation: The Crucial Issue for Man's Ancestry. *Southwestern Journal of Anthropology*, *18*(2), 119–148. https://doi.org/10.1086/soutjanth.18.2.3629013

Back, J., Suzin, A., & Aguiar, L. (2019). Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (Primates: Cebidae). *Zoologia*, *36*, 1–10. https://doi.org/10.3897/zoologia.36.e30845

Bates, et al. 2014.**Fitting linear mixed-effects models using lme4**. arXiv preprint arXiv:1406.5823.

Bateson, M., & Martin, P. (2021). MEASURING BEHAVIOUR: an introductory guide. Cambridge Univ Press.

Bergeson, D. J. (1998). Patterns of Suspensory Feeding in Alouatta palliata, Ateles geoffroyi, and Cebus capucinus. *Springer EBooks*, 45–60. https://doi.org/10.1007/978-1-4899-0092-0_3

Bezanson, M. (2009). Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*. *American Journal of Physical Anthropology*, *140*(3), 508–517. https://doi.org/10.1002/ajpa.21099

Bezanson, M. (2017). Primate Positional Behavior Development and Evolution. *Annual Reviews*, *46*(1), 279–298. https://doi.org/10.1146/annurev-anthro-102116-041503

Bezanson, M. F. (2006). Leap, Bridge, or Ride? Ontogenetic Influences on Positional Behavior in *Cebus* and *Alouatta*. *Kluwer Academic Publishers EBooks*, 333–348. https://doi.org/10.1007/0-387-25872-8_16

Bezanson, M., & Morbeck, M. E. (2013). Future Adults or Old Children? Integrating Life History Frameworks for Understanding Primate Positional Patterns. In *Building Babies* (pp. 435–458). Springer New York, NY.

Boinski, S., & Fragaszy, D. M. (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*. *Animal Behaviour*, *37*, 415–428. https://doi.org/10.1016/0003-3472(89)90089-4

Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M., & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis* and *S. sciureus*). *Behaviour*, *139*(2), 227–261. https://doi.org/10.1163/156853902760102663

Bufalo, F. S., Galetti, M., & Culot, L. (2016). Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America. *International Journal of Primatology*, *37*(3), 333–349. https://doi.org/10.1007/s10764-016-9903-3

Canale, G. R., Kierulff, M. C. M., & Chivers, D. J. (2013). A Critically Endangered Capuchin Monkey (*Sapajus xanthosternos*) Living in a Highly Fragmented Hotspot. *Primates in Fragments*, 299–311. https://doi.org/10.1007/978-1-4614-8839-2_20

Cant, J. G. H. (1986). Locomotion and Feeding Postures of Spider and Howling Monkeys: Field Study and Evolutionary Interpretation. *Folia Primatologica*, *46*(1), 1–14. https://doi.org/10.1159/000156232

Cant, J. G. H. (1992). Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *American Journal of Physical Anthropology*, *88*(3), 273–283. https://doi.org/10.1002/ajpa.1330880302

Cant, J. G. H., Youlatos, D., & Rose, M. D. (2003). Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador. *Journal of Human Evolution*, *44*(6), 685–699. https://doi.org/10.1016/s0047-2484(03)00060-5

Dagosto, M., & Gebo, D. L. (1998). Methodological Issues in Studying Positional Behavior. *Primate Locomotion*, 5–29. https://doi.org/10.1007/978-1-4899-0092-0_1

Doran, D. M. (1992). The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. *Journal of Human Evolution*, *23*(2), 139–157. https://doi.org/10.1016/0047-2484(92)90104-h

Doran, D. M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology*, *91*(1), 83–98. https://doi.org/10.1002/ajpa.1330910106

Druelle, F., Aerts, P., & Berillon, G. (2016). Effect of body mass distribution on the ontogeny of positional behaviors in non-human primates: Longitudinal follow-up of infant captive olive baboons (*Papio anubis*). *American Journal of Primatology*, *78*(11), 1201–1221. https://doi.org/10.1002/ajp.22575

Eppley, T. M., Hoeks, S., Chapman, C. A., Ganzhorn, J. U., Hall, K., Owen, M. A., Adams, D. B., Allgas, N., Amato, K. R., Andriamahaihavana, M., Aristizabal, J. F., Baden, A. L., Balestri, M., Barnett, A. A., Bicca-Marques, J. C., Bowler, M., Boyle, S. A., Brown, M., Caillaud, D., & Calegaro-Marques, C. (2022). Factors influencing terrestriality in primates of the Americas and Madagascar. *Proceedings of the National Academy of Sciences*, *119*(42). https://doi.org/10.1073/pnas.2121105119

Estrada, A., Garber, P. A., & Chaudhary, A. (2020). Current and future trends in socio-economic, demographic and governance factors affecting global primate conservation. *PeerJ*, *8*, e9816. https://doi.org/10.7717/peerj.9816

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M., Gouveia, S., Dobrovolski, R., & Shanee, S. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1). https://doi.org/10.1126/sciadv.1600946

Fleagle, J. G., & Mittermeier, R. A. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology*, *52*(3), 301–314. https://doi.org/10.1002/ajpa.1330520302

Fontaine, R. (1990). Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. *American Journal of Physical Anthropology*, *82*(4), 485–508. https://doi.org/10.1002/ajpa.1330820409

Fontaine, R. P. (1994). Play as physical flexibility training in five ceboid primates. *Journal of Comparative Psychology*, *108*(3), 203–212. https://doi.org/10.1037/0735-7036.108.3.203

Fragaszy, D. M. (1990). Sex and age differences in the organization of behavior in wedge-capped capuchins, *Cebus olivaceus*. *Behavioral Ecology*, *1*(1), 81–94. https://doi.org/10.1093/beheco/1.1.81

Fragaszy, D. M., Elisabetta Visalberghi, & Fedigan, L. M. (2004). *The Complete Capuchin*. Cambridge University Press.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in ecology and evolution, 7(11), 1325-1330.

Gallo, T., Fidino, M., Gerber, B., Ahlers, A. A., Angstmann, J. L., Amaya, M., Concilio, A. L., Drake, D., Gay, D., Lehrer, E. W., Murray, M. H., Ryan, T. J., St Clair, C. C., Salsbury, C. M., Sander, H. A., Stankowich, T., Williamson, J., Belaire, J. A., Simon, K., & Magle, S. B. (2022). Mammals adjust diel activity across gradients of urbanization. *ELife, 11*. https://doi.org/10.7554/elife.74756

Garber, P. A., & Pruetz, J. D. (1995). Positional behavior in moustached tamarin monkeys: effects of habitat on locomotor variability and locomotor stability. *Journal of Human Evolution*, *28*(5), 411–426. https://doi.org/10.1006/jhev.1995.1032

Garber, P. A., & Rehg, J. A. (1999). The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, *110*(3), 325–339. https://doi.org/10.1002/(sici)1096-8644(199911)110:3%3C325::aid-ajpa5%3E3.0.co;2-d

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gebo, D. L. (1992). Locomotor and postural behavior in *Alouatta palliata and Cebus capucinus*. *American Journal of Primatology*, *26*(4), 277–290. https://doi.org/10.1002/ajp.1350260405

Gebo, D. L., & Chapman, C. A. (1995). Positional behavior in five sympatric old world monkeys. *American Journal of Physical Anthropology*, *97*(1), 49–76. https://doi.org/10.1002/ajpa.1330970105

Granatosky, M. C., Young, M. W., Herr, V., Chai, C., Raidah, A., Kairo, J. N., Anaekwe, A., Havens, A., Zou, B., Ding, B., Chen, C., De Leon, D., Shah, H., Valentin, J., Hildreth, L., Castro, T., Li, T., Yeung, A., Dickinson, E., & Youlatos, D. (2022). Positional Behavior of Introduced Monk Parakeets (*Myiopsitta monachus*) in an Urban Landscape. *Animals*, *12*(18), 2372. https://doi.org/10.3390/ani12182372

Gutierres, J. dos S., Radi, L. B. C., Garcia, T. D., Pereira, F. dos S. M., Awane, G. A., & Vidotto-Magnoni, A. P. (2023). Activity budget of a group of black-horned capuchin monkeys (*Sapajus nigritus*) in an urban environment. *Semina: Ciências Biológicas E Da Saúde*, *44*(2), 223–236. https://doi.org/10.5433/1679-0367.2023v44n2p223

Hanna, J. B., Schmitt, D., Wright, K., Eshchar, Y., Visalberghi, E., & Fragaszy, D. (2015). Kinetics of bipedal locomotion during load carrying in capuchin monkeys. *Journal of Human Evolution*, *85*, 149–156. https://doi.org/10.1016/j.jhevol.2015.05.006

Hunt, K. D. (1991). Mechanical implications of chimpanzee positional behavior. *American Journal of Physical Anthropology*, *86*(4), 521–536. https://doi.org/10.1002/ajpa.1330860408

Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates*, *37*(4), 363–387. https://doi.org/10.1007/bf02381373

Izawa, K. (1980). Social behavior of the wild black-capped Capuchin (*Cebus apella*). *Primates*, *21*(4), 443–467. https://doi.org/10.1007/bf02373834

Jakob von Uexküll. (1909). *Umwelt und Innenwelt der Tiere*. Springer Book Archives.

Johnson, S. E., & Shapiro, L. J. (1998). Positional behavior and vertebral morphology in atelines and cebines. *American Journal of Physical Anthropology*, *105*(3), 333–354. https://doi.org/10.1002/(sici)1096-8644(199803)105:3%3C333::aid-ajpa4%3E3.0.co;2-s

Laird, M. F., Punjani, Z., Oshay, R. R., Wright, B. W., Fogaça, M. D., Casteren, A., Izar, P., Visalberghi, E., Fragazy, D., Strait, D. S., Ross, C. F., & Wright, K. A. (2022). Feeding postural behaviors and food geometric and material properties in bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Biological Anthropology*. https://doi.org/10.1002/ajpa.24501

Lawler, R. R. (2006). Sifaka positional behavior: Ontogenetic and quantitative genetic approaches. *American Journal of Physical Anthropology*, *131*(2), 261–271. https://doi.org/10.1002/ajpa.20430.

Lawler, R. R., Ford, S. M., Wright, P. C., & Easley, S. P. (2006). The Locomotor Behavior of *Callicebus brunneus* and *Callicebus torquatus*. *Folia Primatologica*, *77*(3), 228–239. https://doi.org/10.1159/000091232.

Leite, J. R. (2012). *Corredores ecológicos na Reserva da Biosfera do Cinturão Verde de São Paulo: a possibilidade e conflitos.* [Doctoral Dissertation].

Lorenzo, M. P. (2018). *Comportamento e Ecologia de uma População de Macacos-prego (Sapajus nigritus Goldfuss, 1809) em um Fragmento Florestal Inserido em Área Urbana no Município de Londrina, Paraná, Brasil* [Unpublished Master's degree dissertation].

Lousa, T. C., de Grande, T. O., & Mendes, F. D. C. (2022). Time budget and foraging strategies of two provisioned groups of tufted capuchin monkeys, *Sapajus libidinosus*, in a small, seasonal urban forest fragment. *Primates*, *63*(4), 387–395. https://doi.org/10.1007/s10329-022-00993-3

Ludwig, G., de Melo, F. R., Martins, W. P., Lynch Alfaro, J. W., Alonso, A. C., dos Santos, M. C., & Rímoli, J. (2015). *Sapajus nigritus*: Ludwig, G., de Melo, F.R., Martins, W.P., Miranda, J.M.D., Lynch Alfaro, J.W., Alonso, A.C., dos Santos, M.C. & Rímoli, J. *IUCN Red List of Threatened Species*. https://doi.org/10.2305/iucn.uk.2021-1.rlts.t136717a192593806.en

Lüdecke D (2023). sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.15, https://CRAN.R-project.org/package=sjPlot

Lynch Alfaro, J. W., Izar, P., & Ferreira, R. G. (2014). Capuchin monkey research priorities and urgent issues. *American Journal of Primatology*, *76*(8), 705–720. https://doi.org/10.1002/ajp.22269

Martins, W. P., Izar, P., Santos, W., Henrique, F., & Alfaro, J. L. (2022). Diet, activity patterns, and home range use in forest and cultivated areas for one wild group of endangered crested capuchin monkeys (*Sapajus robustus*) in Reserva Natural Vale, Espírito Santo, Brazil. *American Journal of Primatology*, *84*(8). https://doi.org/10.1002/ajp.23413

Mikula, P., Šaffa, G., Nelson, E., & Tryjanowski, P. (2018). Risk perception of vervet monkeys *Chlorocebus pygerythrus* to humans in urban and rural environments. *Behavioural Processes*, *147*, 21–27. https://doi.org/10.1016/j.beproc.2017.12.011

Morbeck, M. E. (1977). Positional behavior, selective use of habitat substrate and associated non-positional behavior in free-ranging *Colobus guereza* (Rüppel, 1835). *Primates, 18*(1), 35–58. https://doi.org/10.1007/bf02382952

Mota, F. M. M., Leite, M. R., & Martins, W. P. (2018). Fragmentation dynamics and loss of area of potential occupancy within the distribution limits of the endangered crested capuchin monkey (*Sapajus robustus*). *American Journal of Primatology*, *80*(9), e22906. https://doi.org/10.1002/ajp.22906

Patterson, L., Kalle, R., & Downs, C. (2018). Factors affecting presence of vervet monkey troops in a suburban matrix in KwaZulu-Natal, South Africa. *Landscape and Urban Planning*, *169*, 220–228. https://doi.org/10.1016/j.landurbplan.2017.09.016

Patterson, L., Kalle, R., & Downs, C. T. (2019). Living in the suburbs: Space use by vervet monkeys (*Chlorocebus pygerythrus*) in an eco-estate, South Africa. *African Journal of Ecology*, *57*(4), 539–551. https://doi.org/10.1111/aje.12629

Perodaskalaki, A., Rammou, D.-L., Thapamagar, T., Bhandari, S., Bhusal, D. R., & Youlatos, D. (2023). Habitat Use and Positional Behavior of Northern Palm Squirrels (*Funambulus pennantii*) in an Urban Forest in Central Nepal. *Land*, *12*(3), 690–690. https://doi.org/10.3390/land12030690

Prates, H. M., & Bicca-Marques, J. C. (2008). Age-Sex Analysis of Activity Budget, Diet, and Positional Behavior in *Alouatta caraya* in an Orchard Forest. *International Journal of Primatology*, *29*(3), 703–715. https://doi.org/10.1007/s10764-008-9257-6

Prost, J. H. (1965). A Definitional System for the Classification of Primate Locomotion. *American Anthropologist*, *67*(5), 1198–1214. http://www.jstor.org/stable/668363

Rahman, Md. M., Jaman, M. F., Khatun, Mst. T., Alam, S. M. I., Ruhul Kayum, A. R. M., & Uddin, M. (2015). Substrate Utilization by Bengal Sacred Langur *Semnopithecus entellus* (Dufresne, 1797) in Jessore, Bangladesh: Effect of Resource Type on Feeding in Urban and Rural Groups. *International Journal of Pure and Applied Zoology* , *3*(2), 0.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Remis, M. J. (1998). The Gorilla Paradox. *Primate Locomotion*, 95–106. https://doi.org/10.1007/978-1-4899-0092-0_6

Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception-action perspective. *Developmental Science*, *11*(6), 828–840. https://doi.org/10.1111/j.1467-7687.2008.00731.x

Ripley, S. (1967). The leaping of langurs: A problem in the study of locomotor adaptation. *American Journal of Physical Anthropology*, *26*(2), 149–170. https://doi.org/10.1002/ajpa.1330260206

Rockström, J. (2009). A Safe Operating Space for Humanity. *Nature*, *461*(7263), 472–475. https://doi.org/10.1038/461472a

Rosenberger, A. L. (1992). Evolution of feeding niches in new world monkeys. *American Journal of Physical Anthropology*, *88*(4), 525–562. https://doi.org/10.1002/ajpa.1330880408

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/

Rudnick, D. A., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C. W., Gerber, L. R., Hartter, J., Jenness, J. S., Kintsch, J., Merenlender, A. M., Perkl, R. M., Preziosi, D. V., & Trombulak, S. C. (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Ecological Society of America*, *16*, 1–23.

Sabbatini, G., Stammati, M., Tavares, M. C. H., Giuliani, M. V., & Visalberghi, E. (2006). Interactions between humans and capuchin monkeys (*Cebus libidinosus*) in the Parque Nacional de Brasília, Brazil. *Applied Animal Behaviour Science*, *97*(2-4), 272–283. https://doi.org/10.1016/j.applanim.2005.07.002

Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2014). Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution*, *66*, 29–38. https://doi.org/10.1016/j.jhevol.2013.09.006

Saunders, E. L. R., Roberts, A. M., & Thorpe, S. K. S. (2018). Positional behavior. *The International Encyclopedia of Biological Anthropology*, 1–7. https://doi.org/10.1002/9781118584538.ieba0392

Schaller, G. B. (1963). *The Mountain Gorilla* (p. 84). THE UNIVERSITY OF CHICAGO.

Suzin, A., Back, J. P., Garey, M. V., & Aguiar, L. M. (2017). The Relationship Between Humans and Capuchins (*Sapajus sp.*) in an Urban Green Area in Brazil. *International*

Journal of Primatology, *38*(6), 1058–1071. https://doi.org/10.1007/s10764-017-9996-3

The IUCN Red List of Threatened Species. (2023). IUCN Red List of Threatened Species; Name. https://www.iucnredlist.org/search?taxonomies=100691&searchType=species

Tuttle, R. (1975). Parallelism, Brachiation, and Hominoid Phylogeny. *Springer EBooks*, 447–480. https://doi.org/10.1007/978-1-4684-2166-8_17

Washburn, S. L. (1950). THE ANALYSIS OF PRIMATE EVOLUTION WITH PARTICULAR REFERENCE TO THE ORIGIN OF MAN. *Cold Spring Harbor Symposia on Quantitative Biology*, *15*(0), 67–78. https://doi.org/10.1101/sqb.1950.015.01.009

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Available from: https://ggplot2.tidyverse.org.

Williamson, R. E., Webb, S. E., Dubreuil, C., Lopez, R., Cheves Hernandez, S., Fedigan, L. M., & Melin, A. D. (2021). Sharing spaces: niche differentiation in diet and substrate use among wild capuchin monkeys. *Animal Behaviour*, *179*, 317–338. https://doi.org/10.1016/j.anbehav.2021.06.002

Wright, K. A. (2007). The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. *American Journal of Primatology*, *69*(7), 736–756. https://doi.org/10.1002/ajp.20391

Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., & Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, *81*(12). https://doi.org/10.1002/ajp.23067

Youlatos, D. (1998). Positional behavior of two sympatric guianan capuchin monkeys, the brown capuchin (*Cebus apella*) and the wedge-capped capuchin (*Cebus olivaceus*). *Mammalia*, *62*(3). https://doi.org/10.1515/mamm.1998.62.3.351

Youlatos, D. (1999). Comparative locomotion of six sympatric primates in Ecuador. *Annales Des Sciences Naturelles - Zoologie et Biologie Animale*, *20*(4), 161–168. https://doi.org/10.1016/s0003-4339(00)88884-x

Youlatos, D. (2002). Positional behavior of black spider monkeys (*Ateles paniscus*) in french guiana. *International Journal of Primatology*, *23*(5), 1071–1093. https://doi.org/10.1023/a:1019602116805

Youlatos, D. (2008). Locomotion and positional behavior of spider monkeys. *Spider Monkeys*, 185–219. https://doi.org/10.1017/cbo9780511721915.007

Zhu, W.-W., Garber, P. A., Bezanson, M., Qi, X.-G., & Li, B.-G. (2014). Age- and sex-based patterns of positional behavior and substrate utilization in the golden snub-nosed monkey (*Rhinopithecus roxellana*). *American Journal of Primatology*, *77*(1), 98–108. https://doi.org/10.1002/ajp.22314