Universidade Estadual de Londrina

EPHRAIM LUIZ DE ANDRADE FRANÇA

ESTRUTURA DA BRINCADEIRA LOCOMOTORA-ROTACIONAL, COM OBJETO E SOCIAL EM JUVENIS DE MACACOS-PREGO-PRETO (*SAPAJUS NIGRITUS*)

Londrina
2021

EPHRAIM LUIZ DE ANDRADE FRANÇA

ESTRUTURA DA BRINCADEIRA LOCOMOTORA-ROTACIONAL, COM OBJETO E SOCIAL EM JUVENIS DE MACACOS-PREGO-PRETO (*SAPAJUS NIGRITUS*)

Dissertação apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina - UEL, como requisito parcial para a obtenção do título de Mestre.

Orientadora: Profa. Dra. Ana Paula Vidotto Magnoni.

Coorientador: Dr. Tiago Falótico.

Londrina
2021

Ficha de identificação da obra elaborada pelo autor, através do Programa de Geração Automática do Sistema de Bibliotecas da UEL

F814 França, Ephraim Luiz de Andrade.

Estrutura da brincadeira locomotora-rotacional, com objeto e social em juvenis de macacos-prego-preto (*Sapajus nigritus*) / Ephraim Luiz de Andrade França. - Londrina, 2021.
66 f. : il.

Orientadora: Ana Paula Vidotto-Magnoni.
Coorientador: Tiago Falótico.
Dissertação (Mestrado em Ciências Biológicas) - Universidade Estadual de Londrina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ciências Biológicas, 2021. Inclui bibliografia.

1. Brincadeira - Tese. 2. Estrutura - Tese. 3. Ontogenia - Tese. 4. Primatas Tese. I. Vidotto-Magnoni, Ana Paula. II. Falótico, Tiago. III. Universidade Estadual de Londrina. Centro de Ciências Biológicas. Programa de Pós-Graduação em Ciências Biológicas. IV. Título.

CDU 577.4

EPHRAIM LUIZ DE ANDRADE FRANÇA

ESTRUTURA DA BRINCADEIRA LOCOMOTORA-ROTACIONAL, COM OBJETO E SOCIAL EM JUVENIS DE MACACOS-PREGO-PRETO (SAPAJUS NIGRITUS)

Dissertação apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina - UEL, como requisito parcial para a obtenção do título de Mestre.

BANCA EXAMINADORA

____

Orientadora: Profa. Dra. Ana Paula Vidotto Magnoni.
Universidade Estadual de Londrina – UEL

____

Profa. Dra. Jessica Ward Lynch
Universidade da Califórnia em Los Angeles – UCLA

____

Profa. Dra. Briseida Dôgo de Resende
Universidade de São Paulo – USP

Londrina, 26 de agosto de 2021.

AGRADECIMENTOS

A todos aqueles que fazem ou fizeram parte do grupo de estudos do Laboratório de Ecologia e Comportamento Animal da Universidade Estadual de Londrina, agradeço pelo apoio, material, dedicação intelectual e física. Foram longas trilhas de mato e conhecimento que percorremos. Em especial agradeço a grandíssima Profa. Dra. Ana Paula Vidotto Magnoni por toda a minha formação como pesquisador e pessoa durante esses anos. Também, ao meu colega de trabalho, mentor e grande amigo Felipe agradeço por me apresentar a primatologia, pelos momentos de campo e por tudo o que vivemos.

Aos meus amigos e todos aqueles para quais dediquei parte do meu espírito e nutriram por mim bons sentimentos, agradeço do maior interior que eu possa expressar. Esses são grande parte do que levo comigo, de forma que, apesar do tempo, o que se é, é resultado de todas as formantes.

Agradeço a Sara, minha mãe, que estando distante de mim se dedicou para que eu estivesse bem e feliz.

Agradeço a José, meu pai, por toda a educação e respeito em mim inculcados.

"O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001”.

França, Ephraim Luiz de Andrade. **Estrutura da brincadeira locomotora-rotacional, com objeto e social em juvenis de macacos-prego-preto (sapajus nigritus).** 2021. 66 f. Dissertação (Mestrado em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina, 2021.

RESUMO

De acordo com a hipótese 'Treinando para o inesperado', animais engajam em auto desvantagem durante a brincadeira, prejudicando ativamente a sua locomoção, posição e sentidos. Nessas situações, os indivíduos aprendem como recuperar o controle, desenvolvendo versatilidade de movimentos e habilidades emocionais. Além disso, indivíduos mais jovens engajariam em mais auto desvantagem durante a brincadeira locomotora-rotacional enquanto que indivíduos mais velhos durante a brincadeira social. Visando testar essa premissa de auto desvantagem durante a ontogenia e verificar a 'Maior imprevisibilidade da brincadeira com objeto em indivíduos jovens', sequências comportamentais de brincadeira geral, locomotora-rotacional, com objeto e social foram amostradas em um grupo de macacos-prego-preto (*Sapajus nigritus*) que habitam um fragmento urbano de Mata Atlântica no Brasil. Sequências de brincadeira geral (N = 18), com objeto (N = 10), locomotora-rotacional (N = 14) e social (N = 23) foram submetidas à análise multivariada 'Detecção e análise de *T-patterns*'. A imprevisibilidade da estrutura - baseada na variabilidade, exageração e repetibilidade - foi comparada entre indivíduos jovens e velhos. Indivíduos jovens engajaram em mais auto desvantagem durante a brincadeira locomotora-rotacional, no entanto, diferenças na imprevisibilidade durante a brincadeira social não foram observadas entre as classes etárias. A hipótese 'Maior imprevisibilidade da brincadeira com objeto em indivíduos jovens' foi apoiada. Assim como outras espécies de primatas que dependem de manipulação extrativa durante o forrageio, indivíduos jovens engajaram em mais comportamentos de manipulação durante a brincadeira e esses padrões foram similares aos observados tardiamente na ontogenia durante a manipulação funcional.

Palavras-chave: desenvolvimento; manipulação; ontogenia; auto desvantagem; *T-pattern*.

FRANÇA, Ephraim Luiz de Andrade. **Locomotor-rotational, object and social play structure in young black-horned capuchin monkeys (*Sapajus nigritus*).** 2021. 66 p. Dissertation (Master's degree in Biological Sciences) – State University of Londrina, Londrina, Brazil, 2021.

ABSTRACT

According to the 'Training for the unexpected' hypothesis, animals engage in self-handicapping during play, actively impairing their locomotion, position and senses. In these situations, individuals learn how to regain control, developing versatility of movements and emotional abilities. Also, younger individuals would engage in more self-handicapping during locomotor-rotational play while older individuals during social play. In order to test this premise of self-handicapping during the ontogeny and verify whether there is a 'Higher unpredictability of object play among young individuals', we sampled behavioral sequences of general, locomotor-rotational, object and social play in a wild group of black-horned capuchin monkeys (*Sapajus nigritus*) living in an Atlantic Forest urban fragment in Brazil. Play sequences for general (N = 18), object (N = 10), locomotor-rotational (N = 14) and social play (N = 23) were submitted to the multivariate 'T-pattern detection and analysis'. We compared the unpredictability of the structure - based on the variability, exaggeration and repeatability - between young and old individuals. Young individuals engaged in more self-handicapping during locomotor-rotational play, however, we observed no differences in social play unpredictability between age classes. We supported the 'Higher unpredictability of object play among young individuals' hypothesis. Such as other primate species that rely on extractive manipulation during foraging, young individuals engaged in more manipulation behaviors during play, and these patterns were similar to those observed in functional manipulation later on the ontogeny.

Keywords: development; manipulation; ontogeny; self-handicapping; T-pattern.

LISTA DE FIGURAS

LISTA DE TABELAS

LISTA DE ABREVIATURAS E SIGLAS

APVM	Ana Paula Vidotto Magnoni
CEUA	Animal Ethics Committee of the State University of Londrina
EAF	Ephraim A. França
e.g.	exempli gratia
H1	Hypothesis 1
H2	Hypothesis 2
i.e.	id est
IQR	Interquartile range
j1	Juvenile 1
j2	Juvenile 2
j3	Juvenile 3
j4	Juvenile 4
L-R	Locomotor-rotational
OI	Old individuals
SD	Standard deviation
TF	Tiago Falótico
TPA	T-pattern detection and analysis
YI	Young individuals

SUMÁRIO

1. APRESENTAÇÃO

Este documento é uma dissertação de mestrado constituída de uma introdução geral do tema e da espécie estudada e de um capítulo. Nesse capítulo são apresentadas análises da estrutura temporal do comportamento de brincadeira na ontogenia de juvenis de macacos-prego-preto (*Sapajus nigritus*). Esse capítulo foi elaborado no formato de manuscrito, que será submetido para a publicação no periódico *International Journal of Primatology*.

2. INTRODUÇÃO

2.1 Definições e funções da brincadeira locomotora-rotacional, social e com objeto

Durante os períodos de infante e juvenil, a brincadeira em primatas é um comportamento intuitivamente distinguível (Graham & Burghardt, 2010). Apesar de seu fácil reconhecimento, as definições da brincadeira são variáveis e pesquisadores visaram categorizá-la baseados em abordagens motivacionais, estruturais e ontogenéticas (Burghardt, 2005; Pellegrini, 2010; Pellis et al., 2015). Entre essas definições, alguns aspectos da brincadeira são recorrentes: a brincadeira é espontaneamente expressa pelo individual, sendo uma atividade prazerosa; a brincadeira não é associada à um resultado ou objetivo; a brincadeira consiste de movimentos exagerados, repetidos e incompletos que se assemelham à comportamentos observados em contextos funcionais; e a brincadeira é geralmente iniciada por um indivíduo imaturo em um ambiente desestressado (Martin & Caro, 1985; Špinka, Newberry & Bekoff, 2001; Burghardt, 2005; Pellegrini, Dupuis, & Smith, 2007; Pellegrini, 2010; Gray, 2019).

Em primatas não-humanos, a brincadeira pode ser categorizada em brincadeira locomotora-rotacional (L-R), com objeto e social (Fagen, 1981; Burghardt, 1998). A primeira é realizada por um único indivíduo e consiste de movimentos vigorosos e exagerados como cambalhotas e balanço durante posturas suspensórias (Bezerra et al. 2011; de Boer et al. 2013). A segunda é um comportamento de brincadeira realizado juntamente com um objeto (e.g. carregar um objeto durante a brincadeira L-R) ou direcionada a um objeto (e.g. golpear um fruto; Petrů et al., 2009; Perry, Barrett & Godoy, 2017). Dois ou mais indivíduos podem engajar em jogos sociais com objeto como o *Toy game*, no qual um ou mais macacos passam um objeto de boca a boca ou de mão em mão (Perry et al., 2017). A terceira envolve dois ou mais indivíduos e consiste de exibições, perseguições, brincadeira de luta, brincadeira sexual (i.e. comportamento sócio-sexual durante a brincadeira) e outros padrões de contato (Rosenblum & Cooper, 1968; Pellis & Pellis, 1997; Bezerra et al. 2011; Birnie et al., 2012; Lutz & Judge, 2017).

Enquanto a brincadeira é consensualmente dita custosa, benefícios que justificariam esse investimento energético ainda são discutíveis (Burghardt, 2005, Graham & Burghardt, 2010; Pellis et al., 2015). Funcionalmente, a brincadeira foi definida como um comportamento responsável pelo desenvolvimento, prática e manutenção de habilidades físicas, cognitivas e sociais (Fagen, 1981). Essa visão é baseada na prevalência do comportamento em juvenis e que como resultado de brincar enquanto jovens, indivíduos adquirem capacidades para realizar os comportamentos funcionais durante a maturidade (Martin & Caro, 1985; Graham & Burghardt, 2010; Pellis et al., 2015). Derivada desse conceito, a hipótese ‘Treino físico ou motor’ afirma que devido aos requerimentos físicos da brincadeira, indivíduos aprimoram a flexibilidade, força e resistência física durante a brincadeira (Bekoff, 1988; Byers, 1998; Pellegrini, 2010). De acordo com a mesma premissa de ‘pagamentos futuros’, a hipótese ‘Brincadeira como prática’ assume que a brincadeira se assemelha à comportamentos funcionais como uma forma de prática de habilidades necessárias no período adulto (Graham & Burghardt, 2010). Evidências para essas hipóteses são poucas e geralmente associativas, já que variáveis e efeitos para longo termo são difíceis de isolar e mensurar (Martin & Caro, 1985). Em um estudo com cinco espécies de Platyrrhini na natureza, o repertório extenso de posturas e modos de locomoção durante a brincadeira L-R foram associados ao treino da flexibilidade (*Alouatta palliata, Ateles geoffroyi, Cacajao calvus, Saimiri boliviensis* e

Cebus capucinus: Fontaine, 1994). A mesma conclusão foi relatada para cinco espécies de macacos. Esses macacos de vida livre apresentaram comportamentos de brincadeira L-R, social e com objeto que foram tanto similares ou dissimilares à padrões utilizados em contextos funcionais. Aqueles que se assemelharam à comportamentos funcionais foram apontados como uma forma de prática nas espécies (*Chlorocebus pygerythrus, Cercopithecus neglectus, Cercopithecus diana, Erythrocebus patas* e *Semnopithecus entellus*: Petrů et al., 2009).

Uma visão alternativa das funções da brincadeira declara que a brincadeira pode resultar em benefícios imediatos (Martin & Caro, 1985; Špinka et al., 2001; Pellegrini et al., 2007; Gray, 2019). Nessa perspectiva, aprender e engajar em comportamentos inovadores é um benefício imediato primário da brincadeira (Pellegrini et al., 2007). Dessa forma, a brincadeira seria uma estratégia de baixo risco para desenvolver capacidades importantes para o cenário atual e futuro dos indivíduos (Pellegrini et al., 2007). Uma abordagem do desenvolvimento e inovação em relação a ontogenia da brincadeira L-R e social é a hipótese ‘Treinando para o inesperado’ (Špinka et al., 2001). De acordo com essa hipótese, a brincadeira em mamíferos possui a função ancestral de aprimorar a versatilidade de movimentos e habilidades emocionais para aprender a lidar com eventos inesperados. Esses benefícios são adquiridos durante a brincadeira, quando indivíduos engajam em sequências comportamentais ‘estranhas’ nas quais eles simulam a perda de controle na locomoção, posição e sentidos. Nessas sequências os indivíduos aprendem a adaptar a locomoção e estados mentais para lidar com essas situações atípicas. Em sequências comportamentais funcionais como perseguição à presa, fuga de um predador ou relações intraespecíficas agonísticas, o animal pode ser desorientado ou interrompido por situações inesperadas como mudanças no ambiente e informação visual, colisões e movimentos do oponente. A habilidade para lidar com essas situações inesperadas pode levar ao sucesso quando o indivíduo tem que lidar com o medo, capturar a presa, escapar de um predador ou em uma contestação de recurso. Durante a brincadeira, indivíduos buscam experienciar o inesperado por meio de auto desvantagem (*self-handicapping*) - ativamente perder o controle locomotor ou engajar em cenários de desvantagem. Visando criar auto desvantagem, os animais engajam em sequências comportamentais altamente imprevisíveis, assumem posturas atípicas, brincam em substratos instáveis, alteram contextos motivacionais (i.e. tipos de brincadeira) e prejudicam as orientações sensoriais e espaciais (Špinka et al., 2001; Petrů et al., 2009; Pellis & Pellis, 2011; Gray, 2019). Espera-se um pico de frequência e auto desvantagem na brincadeira L-R em indivíduos mais jovens e um decréscimo em indivíduos mais velhos, quando estes se tornam mais familiares ao ambiente e há menor necessidade de treinar para o inesperado. Entretanto, a imprevisibilidade e frequência da brincadeira social deve apresentar um pico tardio, devido à altos requerimentos cognitivos da brincadeira social, persistindo durante mais tempo na ontogenia (Špinka et al., 2001).

Em relação à manipulação de objetos em primatas, geralmente ocorre uma expansão do repertório com a idade (Heldstab, 2020). Há um período extenso de brincadeira e exploração com objeto em algumas espécies, resultando em um aprendizado progressivo da manipulação e uso de ferramentas (Resende, Ottoni & Fragaszy, 2008; Tan, 2017; Heldstab, 2020). Em um grupo de vida livre de *Macaca fascicularis*, infantes inicialmente brincam com um item e posteriormente (1.5-2.5 anos), indivíduos começam a combinar objetos. Combinações de objetos e comida sem sucesso e ocasionalmente com sucesso são observados mais tarde durante a ontogenia (2.5-3.5 anos) enquanto que indivíduos mais velhos (4.5 anos) tem maiores taxas de sucesso no uso de ferramentas (Tan, 2017). Em *Sapajus*, o desenvolvimento de capacidades para o uso de ferramentais é observado na seguinte ordem: a manipulação de um objeto, um objeto em relação à um substrato, dois objetos e finalmente, três objetos (Resende & Ottoni, 2002; Resende, Ottoni & Fragaszy, 2008). Os dois primeiros tipos de manipulação são desenvolvidos no primeiro ano de vida, enquanto os outros dois entre 1.5 e 2.5 anos de idade. Em um grupo em semi-liberdade no Parque Ecológico do Tietê em São Paulo, Brasil e em um grupo de vida livre na Fazenda Boa Vista no Piauí, Brasil, esse processo de aprendizado resulta no uso eficiente de ferramentas a partir de 2.5 anos de idade (Eshchar et al., 2016; Resende et al., 2014). Um extenso repertório de manipulação é observado precocemente durante a ontogenia de *Sapajus* (i.e. antes dos 3 anos de idade) e esses indivíduos jovens exploram diversos tipos de manipulação durante o comportamento não funcional (i.e. brincadeira/exploração com objeto, Resende & Ottoni, 2002; Resende, 2004). Indivíduos mais velhos têm maior experiência na manipulação e uso de ferramentas e exibem o repertório em contextos funcionais (e.g. forrageio, quebra de cocos com rochas, gravetos como sondas; Resende & Ottoni, 2002; Coelho et al., 2015; Eshchar et al., 2016).

Enquanto a brincadeira/exploração com objeto em indivíduos jovens é reconhecida como uma importante forma de aprendizado e inovação da manipulação e uso de ferramentas em diversas espécies, hipóteses para benefícios imediatos e futuros da brincadeira social e, principalmente, L-R ainda carecem de investigação e evidência (Resende, Ottoni & Fragaszy, 2008; Tan, 2017; Graham & Burghardt, 2010; Pellis et al., 2015). Além disso, a evidência para a hipótese ‘Treinando para o inesperado’ geralmente abrange a auto desvantagem durante a brincadeira de luta ou é evidência alusiva (Pellis, 2002; Palagi, Antonacci & Cordoni, 2007; Petrů et al., 2009;

Cordoni & Palagi, 2011; Pellis & Pellis, 2011; Lutz & Judge, 2017). Evidência empírica para a auto desvantagem durante a brincadeira L-R e social e sua expressão durante a ontogenia é necessária. Esse estudo testa a hipótese 'Treinando para o inesperado' em relação à estrutura e ontogenia da brincadeira L-R e social em juvenis de *Sapajus nigritus* (Špinka et al., 2001).

2.2 A espécie Sapajus nigritus

O macaco-prego-preto (*Sapajus nigritus*) é uma espécie de primata do novo mundo (Platyrrhini). O gênero *Sapajus* pertence à família Cebidae, juntamente com Callithrichinae e Aotinae e à subfamília Cebinae como grupo irmão de *Cebus* e *Saimiri* (Wang et al., 2019). Macacos-prego-preto são caracterizados por um corpo revestido de pelo marrom escuro, cinza ou preto contrastando com faixas de pelos brancos na face. A cabeça desses animais é escura com tufos pretos evidentes direcionados lateralmente em um formato de 'V' ou direcionados para frente (Fragaszy, Visalberghi & Fedigan, 2004; Lynch-Alfaro, Sousa e Silva Jr., & Rylands, 2012). O gênero é amplamente distribuído na América do Sul, especialmente no Brasil, ocupando diversos habitats como a floresta tropical e subtropical, mangues e ambientes semiáridos nos biomas de Floresta Amazônica e Atlântica, Cerrado e Caatinga (Fragaszy et al., 2004; Lynch-Alfaro et al., 2012). *Sapajus nigritus* habitam áreas de costa e galeria da Floresta Atlântica tropical e subtropical de planície, submontana e montana (Martins et al., 2019). No Brasil, a espécie é distribuída nos estados de Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina e Rio Grande do Sul. Na Argentina, a espécie é restrita ao norte das províncias de Iguazú e Missiones (Fragaszy et al., 2004; Martins et al., 2019). Apesar da tolerância da espécie à mudanças e distúrbios ambientais, a fragmentação e desconexão de hábitats, expansão da matriz urbana, de rodagem e energética, caça e hibridização são fatores que levaram a redução de 30% da população nos últimos 50 anos. A espécie é considerada como Espécie Quase Ameaçada desde 2008 na lista vermelha da IUCN (Martins et al., 2019).

Os indivíduos vivem em grupos sociais que variam de quatro a 40 indivíduos (Izar, 2004; Carosi, Linn & Visalberghi, 2005). Reduções abruptas do tamanho do grupo (e.g. quatro indivíduos) estão relacionadas à dinâmicas de fissão e fusão dos grupos, enquanto a flutuação contínua no tamanho do grupo se relaciona a machos engajando em comportamento periférico e solitário e a emigração e imigração de machos para grupos sociais (Izar, 2004; Carosi et al., 2005). Indivíduos de *Sapajus nigritus* também se agrupam em subgrupos (e.g. quatro indivíduos) durante o forrageio e a alimentação solitária é frequente (Izar, 2004; Izar et al., 2012). No Parque Estadual Carlos Botelho, o tempo dedicado ao forrageio variou com as estações e os animais forragearam mais durante a estação seca. Em contrapartida, o descanso e outras atividades foram mais frequentes durante a estação úmida (Izar et al., 2012). A dieta dos macacos-prego constitui-se primariamente de frutas e os indivíduos consomem diversos tipos de bagas, drupas e frutos encapsulados de diversos tamanhos (Wehnke & Domínguez, 2007). Indivíduos também se alimentam de invertebrados, ovos de aves, pequenos vertebrados, folhas, flores, bulbos e sementes (Izar et al., 2012; Mikich & Liebsch, 2014). A dieta pode variar de acordo com a disponibilidade de frutos e os animais se alimentam mais de folhas durante a estação seca (Izar et al., 2012). Alguns grupos de *Sapajus* desenvolveram tradições de uso de ferramentas para o forrageio (Fragaszy et al., 2004; Falótico e Ottoni, 2016). Essas tradições incluem a utilização de rochas como ferramentas percussivas para abrir castanhas e sementes encapsuladas como *Anacardium occidentale*, *Manihot* spp. e *Cordia rufescens* e a utilização de gravetos como sonda para capturar invertebrados (Falótico & Ottoni, 2016).

A gestação de *Sapajus nigritus* dura aproximadamente 153 dias (Lynch, Ziegler & Strier, 2002). Após o nascimento, o recém-nascido agarra-se fortemente ao pelo da mãe e é capaz de se movimentar instavelmente para alcançar os mamilos (Fragaszy et al., 2004). Os macacos-prego rapidamente ganham peso nas primeiras semanas de vida e há uma redução no aumento de massa após seis meses. As fêmeas atingem o peso de adulto em mais quatro anos enquanto os machos atingem o peso de adulto por volta de seis anos de idade (Fragaszy et al., 2004; Fragaszy et al., 2016). O infante rapidamente aprimora o controle postural e a força corporal nos primeiros meses e passa a explorar o ambiente enquanto passa mais tempo longe da mãe (Fragaszy et al., 2004). Nesse momento (6-19 semanas), o indivíduo tem oportunidade de engajar em brincadeira solitária e social, à medida que a manipulação complexa de objetos é observada mais tardiamente (9-26 semanas, Fragaszy et al., 2004).

2.3 O comportamento de brincadeira na espécie *Sapajus nigritus*

Em conformidade ao padrão comum em primatas, a frequência de todas as categorias de brincadeira em *Sapajus* rapidamente aumenta ao longo da infância, atingindo o pico no início do período juvenil, em *Sapajus* de seis meses a um ano (*Cercopithecus aethiops*: Bramblett, 1978 e Govindarajulu et al., 1993; *Papio anubis*: Chalmers, 1980; *Erythrocebus patas*: Rowel & Chism, 1986; *Sapajus* sp.: Resende & Ottoni, 2002, Paukner & Suomi, 2008 e Lutz & Judge, 2017; *Gorilla gorilla*: Palagi, Antonacci & Cordoni, 2007; *Pan*: Cordoni & Palagi, 2011). Em relação às categorias, a brincadeira L-R e com objeto é mais frequente no início do período juvenil (seis meses a um ano) e reduz-se em juvenis mais velhos, à proporção que a brincadeira social se torna mais frequente tardiamente (dois anos ou mais, Resende & Ottoni, 2002; Lutz & Judge, 2017).

Macacos-prego jovens brincam mais que adultos, entretanto, existem diferenças significativas nas taxas observadas em grupos de vida livre e cativos (Fragaszy et al., 2004). As demandas nutricionais e de deslocamento em macacos-prego de vida livre resultam em menor disponibilidade temporal para brincadeira e mais tempo investido em forrageio e deslocamento (Visalberghi & Guidi, 1998; Paukner & Suomi, 2008; Frequência de brincadeira em *Sapajus* de vida livre: Wright et al., 2019: 1.6%). Por outro lado, em grupos cativos, juvenis dedicam grande parte do dia para a brincadeira (Frequência de brincadeira em *Sapajus* cativos: Visalberghi & Guidi, 1998: 43,4%; Fragaszy et al., 2004: 21-24%; Paukner & Suomi, 2008: 9.2%). Em relação ao sexo, juvenis machos tendem a brincar mais que fêmeas e taxas significativamente maiores de brincadeira social (i.e. perseguição e brincadeira de luta) foram encontradas em machos (Paukner & Suomi, 2008). Essa diferença foi apontada como relacionada à hipótese de treino motor, como mais brincadeira de luta e perseguição em juvenis machos estão associadas a maiores frequências de conflitos na maturidade e poderiam ser uma forma de prática em machos imaturos (Paukner & Suomi, 2008). Contudo, diferenças de sexo na frequência de brincadeiras não foram observadas por alguns pesquisadores (Visalberghi & Guidi, 1998). E em relação à composição do grupo, o número de juvenis é particularmente importante pois indivíduos jovens tem forte preferência por brincadeiras com indivíduos jovens em detrimento de subadultos e adultos (Visalberghi & Guidi, 1998; Resende & Ottoni, 2002).

O repertório de brincadeira em macacos-prego é extenso para todos os tipos de brincadeira. A brincadeira L-R inclui diversas acrobacias como girar, pendurar, balançar, saltar e outros movimentos como galopar, rolar, deslizar em superfícies e cambalhotas (Visalberghi & Guidi, 1998; Paukner & Suomi, 2008; Lutz & Judge, 2017). Na brincadeira com objeto, os macacos manipulam objetos naturais como rochas, gravetos e folhas e antrópicos como plástico e metal de enriquecimento ambiental no cativeiro (Resende & Ottoni, 2002; Paukner & Suomi, 2008). A manipulação de objeto inclui arremessar, esfregar, bater, mastigar, empurrar e rasgar objetos (Resende & Ottoni, 2002; Lutz & Judge, 2012). A manipulação se torna mais complexa com a idade. No início da manipulação, infantes manipulam um objeto (manipulação simples) e depois engajam em manipulação combinatória 1 (um objeto em uma superfície), 2 (dois objetos) e 3 (dois ou mais objetos e uma superfície; Resende & Ottoni, 2002; Resende et al., 2008). A brincadeira social é comumente considerada como brincadeira de luta ou perseguição, no entanto, outros padrões sociais e de contato são considerados brincadeira social. A brincadeira de luta consiste de diversos tipos de movimentos e golpes como agarrar a cabeça e membros, tapas, avanço, imobilização, mordida, empurrão e retiradas. A brincadeira social também inclui movimentos menos intensos como luta de baixa intensidade e comportamentos sociossexuais como exibições, abraços e montas (Lynch, 2008; Lutz & Judge, 2017).

Nesse estudo, a estrutura temporal e repertório da brincadeira L-R, com objeto e social (exceto brincadeira de luta) em macacos-prego-preto (*Sapajus nigritus*) foi examinada. Foram testadas duas hipóteses: ‘Treinando para o inesperado’ (Hipótese 1) e ‘Maior imprevisibilidade da brincadeira com objeto em indivíduos jovens’ (Hipótese 2). Segundo a hipótese ‘Treinando para o inesperado’, os animais engajam em sequências de brincadeira com uma estrutura imprevisível, aleatória e alteram entre diferentes contextos comportamentais (i.e. tipos de brincadeira) e interactantes.

A imprevisibilidade na brincadeira é importante para que o animal se habitue e lide com alterações repentinas, que podem acontecer em contextos funcionais como durante uma luta, fuga de um predador ou perseguição à uma presa. Além disso, indivíduos mais jovens, que possuem menor conhecimento e domínio do ambiente, engajariam em maior imprevisibilidade durante a brincadeira L-R do que indivíduos mais velhos, que já estão habituados e para os quais há menor necessidade de treinar para o inesperado. Indivíduos mais velhos também apresentariam maior imprevisibilidade na brincadeira social, já que esse aspecto está relacionado à uma maior capacidade cognitiva (Špinka et al., 2001). A imprevisibilidade da brincadeira em indivíduos jovens (seis meses a três anos) e velhos (três a cinco anos) foi avaliada por meio da análise de três fatores estruturais: variabilidade, exageração e repetibilidade. Essas são características intrínsecas da brincadeira e são diretamente proporcionais a imprevisibilidade das sequências comportamentais (Burghardt, 2005; Resende et al., 2014; Cenni et al., 2020). Dessa forma, espera-se que os indivíduos de diferentes classes etárias engajem igualmente em sequências imprevisíveis de brincadeira, alterando tipos de brincadeira e interactantes. Portanto, espera-se similar variabilidade, exageração e repetibilidade da brincadeira geral nas classes etárias (Predição 1). Também, espera-se que indivíduos jovens apresentem mais imprevisibilidade na brincadeira L-R e, portanto, maior variabilidade, exageração ou repetibilidade durante a brincadeira L-R (Predição 2). Em relação a brincadeira social, espera-se maior variabilidade, exageração ou repetibilidade em indivíduos velhos (Predição 3). Para mais detalhes sobre a hipótese 'Treinando para o inesperado' verificar o Capítulo 1.

A segunda hipótese 'Maior imprevisibilidade da brincadeira com objeto em indivíduos jovens' é relativa a ontogenia da brincadeira com objeto e manipulação funcional. Em macacos-prego, indivíduos mais jovens usualmente engajam em um repertório manipulativo mais extenso e maior imprevisibilidade durante a brincadeira que indivíduos mais velhos (Resende & Ottoni, 2002; Resende et al., 2014). Os indivíduos mais velhos, habituados aos objetos e habilidades manipulativas, gradualmente reduzem o repertório da manipulação não funcional e retêm a manipulação durante o forrageio (Resende & Ottoni, 2002; Resende et al., 2014). Espera-se que a variabilidade, exageração e repetibilidade sejam maiores em indivíduos jovens do que velhos durante a brincadeira com objeto (predição 4). Além disso, o repertório de brincadeira com objeto deve ser maior em indivíduos jovens (Predição 5). Para mais detalhes sobre a hipótese 'Maior imprevisibilidade da brincadeira com objeto em indivíduos jovens' verificar o Capítulo 1.

3. REFERÊNCIAS

Bekoff, M. (1988). Motor Training and Physical Fitness: Possible Short- and Long-Term Influences on the Development of Individuals Differences in Behavior. *Developmental Psychobiology*, 21, 6. https://doi.org/10.1002/dev.420210610.

Bezerra, B.M., Barnett, A.A., Souto, A., & Jones, G. (2011). Ethogram and Natural History of Golden-backed Uakaris (*Cacajao melanocephalus*). *International Journal of Primatology*, 32, 46-68. https://doi.org/10.1007/s10764-010-9435-1.

Birnie, A.K., Hendricks, S.E., Smith, A.S., Milam, R., & French J.A. (2012). Maternal gestational androgens are associated with decreased juvenile play in white-faced marmosets (*Callithrix geoffroyi*). *Hormones and Behavior*, 62, 136-145. https://doi.org/10.1016/j.yhbeh.2012.05.014.

Bramblett, C.A. (1978). Sex differences in the acquisition of play among juvenile Vervet Monkeys. In Smith, E.O. (Ed.), Social Play in Primates (pp. 33-48). New York: Academic Press.

Burghardt, G.M. (1998). The evolutionary origins of play revisited: lessons from turtles. In Bekoff, M. & Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative and Ecological Perspectives (pp. 1-26). Cambridge: Cambridge University Press.

Burghardt, G.M. (2005). The Genesis of Animal Play: Testing the Limits. Cambridge, Massachussets: The MIT Press.

Byers, J.A. (1998). Biological effects of locomotor play: getting into shape, or something more specific? In Bekoff, M. & Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative and Ecological Perspectives (pp. 205-220). Cambridge: Cambridge University Press.

Carosi, M., Linn, G.S., & Visalberghi, E. (2005). The Sexual Behavior and Breeding System of Tufted Capuchin Monkeys (*Cebus apella*). *Advances in the Study of Behavior*, 35, 105-149. https://doi.org/10.1016/S0065-3454(05)35003-0.

Cenni, C., Casarrubea, M., Gunst, N., Vasey, P.L., Pellis, S.M., Wandia, I.N., & Leca, J. (2020). Inferring functional patterns of tool use behavior from the temporal structure of object play sequences in a non-human primate species. *Physiology & Behavior*, 222, 112938. https://doi.org/10.1016/j.physbeh.2020.112938

Chalmers, N.R. (1980). The ontogeny of play in feral Olive Baboons (*Papio Anubis*). *Animal Behavior*, 28, 570-585. https://doi.org/10.1016/S0003-3472(80)80066-2.

Coelho, C.G., Falótico, T., Izar, P., Mannu, M., Resende, B.D., Siqueira, J.O., & Ottoni, E.B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, 18, 911-919. https://doi.org/10.1007/s10071-015-0861-5.

Cordoni, G. & Palagi, E. (2011). Ontogenetic Trajectories of Chimpanzee Social Play Similarities with Humans. *PLoS ONE*., 6, 11. https://doi.org/10.1371/journal.pone.0027344.

De Boer, R.A., Overduin-de-Vries, A.M., Louwerse, A.T., & Sterck, E.H.M. (2013). The Behavioral Context of Visual Displays in Common Marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 75, 1084-1095. https://doi.org/10.1002/ajp.22167.

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Fragaszy, D. (2016). When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, 19. 605-618. https://doi.org/10.1007/s10071-016-0965-6.

Fagen, R. (1981). Animal Play Behavior. Oxford: Oxford University Press.

Falótico, T. & Ottoni, E.B. (2016). The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour*, 153, 4, 421-442. https://doi.org/10.1163/1568539X-00003357.

Fontaine, R. (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., Visalberghi, E., & Fedigan, L.M. (2004). The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge: Cambridge University Press.

Fragaszy, D.M., Izar, P., Liu, Q., Eshchar, Y., Young, L.A., & Visalberghi, E. (2016). Body Mass in Wild Bearded Capuchins, (*Sapajus libidinosus*): Ontogeny and Sexual Dimorphism. *American Journal of Primatology*, 78, 473-484. https://doi.org/10.1002/ajp.22509.

Govindarajulu, P., Hunte, W., Vermeer, L.A., & Horrocks, J.A. The Ontogeny of Social Play in a Feral Troop of Vervet Monkeys (*Cercopithecus arthiops sabaeus*): The Function of Early Play. *International Journal of Primatology*, 14, 5, 701-719. https://doi.org/10.1007/BF02192187.

Graham, K.L. & Bughardt, G.M. (2010). Current perspectives on the Biological Study of Play: Signs of Progress. *The Quarterly Review of Biology*, 85, 4, 393-418. https://doi.org/10.1086/656903.

Gray, P. (2019). Evolutionary Functions of Play: Practice, Resilience, Innovation and Cooperation. In Smith, P.K. & Roopnarine, J.L. (Eds.), The Cambridge Handbook of Play, Developmental and Disciplinary Perspectives (pp. 84-102). Cambridge: Cambridge University Press.

Heldstab, S.A., Isler, K., Schuppli, C., & van Schaik, C.P. (2020). When ontogeny recapitulates phylogeny: Fixed neurodevelopmental sequences of manipulative skills among primates. *Science advances*, 6, 30, eabb4685. https://doi.org/ 10.1126/sciadv.abb4685.

Izar, P. (2004). Female social relationships of *Cebus apella nigritus* in a southeastern Atlantic forest: An analysis through ecological models of primate social evolution. *Behaviour*, 141, 71-99. https://doi.org/10.1163/156853904772746619.

Izar, P., Verderane, M.P., Peternelli-dos-Santos, L., Mendonça-Furtado, O., Presotto, A., Tokuda, M., Visalberghi, E., & Fragaszy, D. (2012). Flexible and Conservative Features of Social Systems in Tufted Capuchin Monkeys: Comparing the Socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. *American Journal of Primatology*, 74, 315-331. https://doi.org/10.1002/ajp.20968, Lutz, M.C. & Judge, P.G. (2017). Self-handicapping during play fighting in capuchin monkeys (*Cebus apella*). *Behaviour*, 154, 9-10, 909-938. https://doi.org/10.1163/1568539X-00003449.

Lynch, J.W., Ziegler, T.E., & Strier, K.B. (2002). Individual and Seasonal Variation in Fecal Testosterone and Cortisol Levels of Wild Male Tufted Capuchin Monkeys, *Cebus apella nigritus. Hormones and Behavior*, 41, 275-287. https://doi.org/10.1006/hbeh.2002.1772.

Lynch Alfaro, J. W. (2008). Scream-Embrace Displays in Wild Black-Horned Capuchin 545 Monkeys. American Journal of Primatology, 70, 551-559. https://doi.org/10.1002/ajp.20528. Špinka, M., Newberry, R.C., & Bekoff, M. (2001). Mammalian play: Training for the Unexpected. *The Quartely Review of Biology*, 76, 2, 141-168. https://doi.org/ 10.1086/393866.

Lynch-Alfaro, J.W., Sousa e Silva Jr., J., & Rylands, A.B. (2012). How Different Are Robust and Gracile Capuchin Monkeys? An Argument for the Use of *Sapajus* and *Cebus*. *American Journal of Primatology*, 74, 273-286. https://doi.rog/ 10.1002/ajp.22007.

Martin, P. & Caro, T.M. (1985). On the Functions of Play and Its Role in Behavioral Development. *Advances in the Study of Behavior*, 15, 59-103. https://doi.org/10.1016/S0065-3454(08)60487-8.

Martins, J.N., dos Santos, M., Lynch Alfaro, J., Martins, W.P., Ludwig, G., Melo, F., Miranda, J., Alonso, A.C. & Rímoli, J. (2019). *Sapajus nigritus*. *The IUCN Red List of Threatened Species 2019*, e.T136717A70614508. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T136717A70614508.en.

Mikich, S.B. & Liebsch, D. (2014). Damage to forest plantations by tufted capuchin (*Sapajus nigritus*): Too many monkeys or not enough fruits? *Forest Ecology and Management*, 314, 9-16. https://doi.org/10.1016/j.foreco.2013.11.026.

Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of Social Play in Juvenile Lowland Gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology*, 49, 4, 433-445. https://doi.org/10.1002/dev.20219.

Paukner, A., & Suomi, S.J. (2008). Sex differences in play behavior in juvenile tufted capuchin monkeys (*Cebus apella*). *Primates*, 49, 288-291. https://doi.org/10.1007/s10329-008-0095-0.

Pellegrini, A.D. (2010). The Development and Function of Locomotor Play. In Nathan, P. & Pellegrini, D. (Eds.), The Oxford Handbook of Play. Oxford: Oxford University Press. https://doi.org/10.1093/oxfordhb/9780195393002.013.0014.

Pellegrini, A.D., Dupuis, D., & Smith, P.K. (2007). Play in evolution and development. *Developmental review*, 27, 261-276. https://doi.org/10.1016/j.dr.2006.09.001.

Pellis, S.M. & Pellis, V.C. (1997). Targets, Tactics, and the Open Mouth Face During Play Fighting in Three Species of Primates. *Aggressive Behavior*, 23, 41-57. https://doi.org/10.1002/(SICI)1098-2337(1997)23:1<41::AID-AB5>3.0.CO;2-W.

Pellis, S.M. (2002). Sex Differences in Play Fighting Revisited: Traditional and Nontraditional Mechanisms of Sexual Differentiation in Rats. *Archives of Sexual Behavior*, 31, 1. https://doi.org/ 10.1023/a:1014070916047.

Pellis, S.M. & Pellis, V.C. (2011). To Whom the Play Signal Is Directed: A Study of Headshaking in Black-Handed Spider Monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology*, 125, 1. https://doi.org/ 10.1037/a0020547.

Pellis, S.M., Burghardt, G.M., Palagi, E., & Mangel, M. (2015). Modeling play: distinguishing between origins and current functions. *Adaptive Behavior*, 23, 6, 331-339. https://doi.org/10.1177/1059712315596053.

Perry, S.E., Barrett, B.J., & Godoy, I. (2017). Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 30, 7806-7813. https://doi.org/10.1073/pnas.1620739114.

Petrů M., Špinka, M., Charvátová, V., & Lhota, S. (2009). Revisiting Play Elements and Self-Handicapping in Play: A Comparative Ethogram of Five Old World Monkey Species. *Journal of Comparative Psychology*, 123, 3, 250-263. https://doi.org/10.1037/a0016217.

Resende, B.D. & Ottoni, E.B. (2002). Brincadeira e aprendizagem do uso de ferramentas em macacos-prego (*Cebus apella*). *Estudos de Psicologia*, 7, 1, 173-180. https://doi.org/10.1590/S1413-294X2002000100018.

Resende, B.D. (2004). Ontogenia de comportamentos manipulativos em um grupo de macacos-prego (*Cebus apella*) em situação de semiliberdade [Doctoral thesis, University of São Paulo]. USP Digital Library. https://doi.org/10.11606/T.47.2004.tde-03062008-140907.

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.

Resende, B.D., Nagy-Reis, M.B., Lacerda, F.N., Pagnotta, M & Savalli, C. (2014). Tufted capuchin monkeys (*Sapajus* sp) learning how to crack nuts: Does variability decline throughout development? *Behavioural Processes*, 109, 89-94. https://doi.org/10.1016/j.beproc.2014.09.002.

Rosenblum, L.A. & Cooper, R.W. (1968). The Squirrel Monkey. New York: Academic Press, Inc.

Rowel, T.E. & Chism, J. (1986). The Ontogeny of Sex Differences in the Behavior of Patas Monkeys. *International Journal of Primatology*, 7, 1, 83-107. https://doi.org/10.1007/BF02692310.

Špinka, M., Newberry, R.C., & Bekoff, M. (2001). Mammalian play: Training for the Unexpected. *The Quartely Review of Biology*, 76, 2, 141-168. https://doi.org/ 10.1086/393866.

Tan, A.W.Y. (2017). From Play to Proficiency: The Ontogeny of Stone-Tool Use in Coastal-Foraging Long-Tailed Macaques (*Macaca fascicularis*) From a Comparative

Perspection-Action Perspective. *Journal of Comparative Psychology*, 131, 2. https://doi.org/10.1037/com0000068.

Visalberghi, E. & Guidi, C. (1998). Play Behaviour in Young Tufted Capuchin Monkeys. *Folia Primatologica*, 69, 419-422. https://doi.org/10.1159/000021665.

Wang, X., Lim, B.K., Ting, N., Hu, J., Liang, Y., Roos, C., & Yu, L. (2019). Reconstructing the phylogeny of new world monkeys (Platyrrhini): evidence from multiple non-coding loci. *Current Zoology*, 65, 5, 579-588. https://doi.org/10.1093/cz/zoy072.

Wehnke, E.V. & Dominguez, C.A. (2007) Seed dispersal ecology of non-restricted frugivores, capuchin monkeys in three neotropical forests. *Journal of Tropical Ecology*, 23, 519-528. https://doi.org/10.1017/S0266467407004257.

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, e23067. https://doi.org/10.1002/ajp.23067.

International Journal of Primatology
Submission Guidelines: https://www.springer.com/journal/10764/submission-guidelines.

Age differences in play behavior in young black-horned capuchin monkeys: 'Training for the unexpected'?

Ephraim A. França[1], Tiago Falótico[2,3], Ana Paula Vidotto-Magnoni[1,4]

[1]Biological Sciences Postgraduate Program, State University of Londrina, Biological Sciences Center, Rd. Celso Garcia Cid, PR 445, CEP 86057-970 – Londrina, Paraná, Brazil.

[2] School of Arts, Sciences and Humanities, University of São Paulo, Av. Arlindo Bettio, 1000, CEP 03828-000 - São Paulo, São Paulo, Brazil.

[3]Neotropical Primates Research Group, São Paulo, Brazil.

E-mail: anavidotto@uel.br; ORCID: 0000-0003-1819-7019; +55 43 3371 4247.

[4]State University of Londrina, Biological Sciences Center, Department of Animal and Vegetal Biology, Rd. Celso Garcia Cid, PR 445, CEP 86057-970 – Londrina, Paraná, Brazil.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. T.F. was supported by grants #2019/00716-2 and #2018/01292-9, São Paulo Research Foundation (FAPESP).

Author Contributions

EAF, TF and APVM conceived and designed the study. EAF conducted the field work, analyses and wrote the manuscript. APVM and TF supervised EAF and provided editorial advice. APVM gave final approval and secured the funding to support the work. All authors discussed the results, edited and approved the manuscript.

Age differences in play behavior in young black-horned capuchin monkeys: 'Training for the unexpected'?

Abstract

According to the ‘Training for the unexpected’ hypothesis, animals engage in self-handicapping during play, actively impairing their locomotion, position and senses. In these situations, individuals learn how to regain control, developing versatility of movements and emotional abilities. Also, younger individuals would engage in more self-handicapping during locomotor-rotational play while older individuals during social play. In order to test this premise of self-handicapping during the ontogeny and verify whether there is a ‘Higher unpredictability of object play among young individuals’, we sampled behavioral sequences of general, locomotor-rotational, object and social play in a wild group of black-horned capuchin monkeys (*Sapajus nigritus*) living in an Atlantic Forest urban fragment in Brazil. Play sequences for general (N = 18), object (N = 10), locomotor-rotational (N = 14) and social play (N = 23) were submitted to the multivariate ‘T-pattern detection and analysis’. We compared the unpredictability of the structure - based on the variability, exaggeration and repeatability - between young and old individuals. Young individuals engaged in more self-handicapping during locomotor-rotational play, however, we observed no differences in social play unpredictability between age classes. We supported the ‘Higher unpredictability of object play among young individuals’ hypothesis. Such as other primate species that rely on extractive manipulation during foraging, young individuals engaged in more manipulation behaviors during play, and these patterns were similar to those observed in functional manipulation later on the ontogeny.

Keywords: Development; Manipulation; Ontogeny; Self-handicapping; T-pattern.

Introduction

Throughout primate infant and juvenile stages, play is a common and intuitively distinguished pattern (Graham & Burghardt, 2010). Despite its ease recognition, definitions of play are variable, and researchers have approached its categorization based on motivational, structural and ontogenetic features (Burghardt, 2005; Pellegrini, 2010; Pellis et al., 2015). Among these definitions, some aspects of play are recurrent: play is spontaneously expressed by the individual, being a pleasurable activity; play is not associated to an outcome, an objective, rather it is done for its 'own sake'; play consists of exaggerated, repeatable and incomplete motor patterns that resemble behaviors observed in functional contexts; and play is generally conducted by an immature individual in a stress-relieved environment (Martin & Caro, 1985; Špinka, Newberry & Bekoff, 2001; Burghardt, 2005; Pellegrini, Dupuis, & Smith, 2007; Pellegrini, 2010; Gray, 2019). These characteristics, despite not universal, are appropriate for an operational definition of play in this study (Burghardt, 2005; Gray, 2019).

Play behavior in non-human primates can be grouped in locomotor-rotational (L-R), object and social play (Fagen, 1981; Burghardt, 1998). L-R play is performed by one individual and consists of vigorous and exaggerated movements such as somersaults and acrobatic swaying postures (Bezerra et al. 2011; de Boer et al. 2013). Object play is an object-assisted (e.g. carrying an object during L-R) or object-directed (e.g. hitting a fruit) behavior (Petrů et al., 2009; Perry, Barrett and Godoy, 2017). Two or more individuals can engage in social object play games like the 'Toy game', in which two or more monkeys pass an object from mouth to mouth or hand to hand (Perry et al., 2017). Social play involves two or more players and consists of displays, chasing, rough and tumble play (i.e. fight play), sexual play (i.e. sociosexual behavior during play) and other contact patterns (Rosenblum & Cooper, 1968; Pellis & Pellis, 1997; Bezerra et al. 2011; Birnie et al., 2012; Lutz & Judge, 2017).

While play is assumed to be costly, benefits that would explain such energetic investment are part of an unsettled discussion (Burghardt, 2005, Graham & Burghardt, 2010; Pellis et al., 2015). Functionally, play was defined as a behavior responsible for the development, practice and maintenance of physical, cognitive and social abilities (Fagen, 1981). This view is based on the prevalence of the behavior in juveniles, and that as a result of playing while young, individuals acquire capabilities to perform functional behaviors later in the ontogeny (Martin & Caro, 1985; Graham & Burghardt, 2010; Pellis et al., 2015). Derived from this view, the 'Physical or motor training' hypothesis affirms that due to the physical requirements of play, individuals enhance physical flexibility, strength and endurance during play (Bekoff, 1988; Byers, 1998; Pellegrini, 2010). According to the same delayed pay-off premise, the hypothesis 'Play as practice' assumes that play resemble functional behaviors as a form of practicing adult skills (Graham & Burghardt, 2010). Evidence for these hypotheses is short and often associative, as variables and outcomes for long-term are difficult to isolate and measure (Martin & Caro, 1985). In a study with five Platyrrhini species in wild, the extensive repertoire of postures and locomotor modes during L-R play were associated to flexibility training (*Alouatta palliata, Ateles geoffroyi, Cacajao calvus, Saimiri boliviensis* and *Cebus capucinus*: Fontaine, 1994). The same conclusion was reported for five monkey species. These free-ranging monkeys presented behaviors in L-R, social and object play that were either similar or dissimilar to patterns used in serious contexts. Those that resembled functional behaviors were pointed to be a form practice in the species (*Chlorocebus pygerythrus, Cercopithecus neglectus, Cercopithecus diana*, *Erythrocebus patas* and *Semnopithecus entellus:* Petrů et al., 2009).

An alternative view of play functions states that play may result in immediate benefits (Martin & Caro, 1985; Špinka et al., 2001; Pellegrini et al., 2007; Gray, 2019). In this perspective, learning and engaging in innovative behavior is a primary immediate benefit of play (Pellegrini et al., 2007). Play, therefore, would be a low-risk strategy to develop several important capabilities for the current and subsequent environments (Pellegrini et al., 2007). An approach on the development and innovation, regarding the ontogeny of L-R and social play is the 'Training for the unexpected' hypothesis (Špinka et al., 2001). According to this hypothesis, mammalian play behavior has a major ancestral function of enhancement of the versatility of movements and emotional abilities for learning to deal with unexpected events. These benefits are acquired during play, when animals engage in 'awkward' behavioral sequences in which they simulate the loss of control in locomotion, position and senses. In these sequences, animals learn how to adapt their locomotion and mental states to deal with these atypical situations. In functional behavioral sequences such as prey chasing, fleeing from a predator or intraspecific agonism, the animal may be disoriented or interrupted by unexpected situations such as changes in the environment and visual input, collisions and opponent movements. The ability to cope with these unexpected situations can lead to success when dealing with fear, in hunting prey, in fleeing from a predator, or in contest competition. During play, individuals seek to experience the unexpected through self-handicapping, or the active loss of the locomotor control and engaging in/entering into disadvantageous scenarios. In order to self-handicap, animals engage on highly unpredictable (i.e. unconstrained, random) behavior sequences, assume atypical postures, play on unstable grounds, change motivational contexts (i.e. types of play) and impair sensory and spatial orientations (Špinka et al., 2001; Petrů et al., 2009; Pellis & Pellis, 2011; Gray, 2019). L-R play self-handicapping and frequency are expected to peak at young ages and decrease or cease in older individuals, when one becomes more familiar with the environment and there is less need to train for the unexpected. However, social play unpredictability and frequencies should peak later in life, as social play demands higher cognitive capabilities and persists longer during ontogeny (Špinka et al., 2001).

Regarding object manipulation in primates, generally there is an expansion of the repertoire with age (Heldstab, 2020). There is an extensive period of object play and exploration in some species, resulting in a progressive learning of manipulation and tool use capabilities (Resende, Ottoni & Fragaszy, 2008; Tan, 2017; Heldstab, 2020). In a *Macaca fascicularis* free-ranging group, infants initially play with single items and posteriorly (1.5-2.5 years) individuals begin to combine objects. Unsuccessful and some successful bouts combining tools and food are observed latter during the ontogeny (2.5-3.5 years) while older individuals (4.5 years) are more successful in the tool usage (Tan, 2017). In *Sapajus,* the development of tool use capabilities develops in the following order: the manipulation of one object, one object on a substrate, two objects and finally three objects (Resende & Ottoni, 2002; Resende, Ottoni & Fragaszy, 2008). The first two types of manipulation are developed in the first year of life, while the two latter within a 1.5-year-old and 2.5-year-old window. In a semi-free group in Tiete Ecological Park, southeastern Brazil and in a free-ranging group at Fazenda Boa Vista, northeastern Brazil, this learning process result in efficient tool use at the end of the 2.5-year period (Eshchar et al., 2016; Resende et al., 2014). A large manipulation repertoire is observed early during the ontogeny of *Sapajus* (i.e. before 3 years old), and these young individuals explore various types of manipulation during non-functional behavior (i.e. object play/exploration, Resende & Ottoni, 2002; Resende, 2004). Older individuals are more experienced at manipulation and tool usage, and exhibit the repertoire in functional contexts (e.g. nut cracking with stones, probe stick; Resende & Ottoni, 2002; Coelho et al., 2015; Eshchar et al., 2016).

While object play/exploration in young individuals is recognized as an important form of learning and innovating manipulation and tool usage in several species, hypothesis for immediate and delayed benefits of social non-fighting and specially L-R play still require further investigation and evidence (Resende, Ottoni & Fragaszy, 2008; Tan, 2017; Graham & Burghardt, 2010; Pellis et al., 2015). Also, evidence for the ‘Training for the unexpected hypothesis’ generally scope self-handicapping during fight play or is only allusive (Pellis, 2002; Palagi, Antonacci & Cordoni, 2007; Petrů et al., 2009; Cordoni & Palagi, 2011; Pellis & Pellis, 2011; Lutz & Judge, 2017). Empirical evidence for self-handicapping during L-R and social non-fighting play and its expression during the ontogeny is still required. The present study tests the ‘training for the unexpected’ hypothesis, regarding the structure and ontogeny of L-R and social play behavior in young *Sapajus nigritus* (Špinka et al., 2001).

In order to evaluate ontogenetic differences in play behavior among young black-horned capuchin monkeys (*Sapajus nigritus*), we examined the structural unpredictability (i.e.

unconstraining, randomness) in four types of play sequences (General, L-R, object and social play). We used the 'T-pattern detection and analysis' (TPA), a multivariate approach that detect significant temporal associations between successive behaviors in a behavioral sequence. These temporal associations form temporal patterns, namely T-patterns (Magnusson, 2016). We compared the following quantitative factors of T-patterns: variability (the number of different T-patterns detected in a sequence), exaggeration (the number of behaviors that form T-patterns, or the length of each pattern detected in a sequence) and repeatability (the number of occurrences of each T-pattern in a sample; Casarrubea et al. (2015); Cenni et al., 2020). When comparing non-functional (i.e. play) to functional sequences, these factors tend to be high, characterizing unpredictable, unconstrained and non-optimal sequences, a general trend in play (Burghardt, 2005; Resende et al., 2014; Cenni et al., 2020; Gunst et al., 2020). Thus, if an individual self-handicaps in play by changing motivational contexts and engaging in unpredictability, then we expect to find sequences with high variability, high exaggeration and high repeatability.

To test the 'Training for the unexpected' hypothesis (Hypothesis 1), self-handicapping is compared among age classes in two ways: measuring unpredictable changes in play types and partners (i.e. motivational contexts) and measuring unpredictability of movements. In general play sequences we expect individuals of all ages to equally self-handicap through unpredictable sequences of play types and partners. Therefore, structure will be similar in variability, exaggeration and repeatability across age classes (Prediction 1). L-R play self-handicapping is expected to peak earlier during the ontogeny and decrease with age, as older individuals are expected to be more experienced with the environment and would have less need to train for the unexpected; thus, we expect young individuals to be less constrained in their L-R sequences. Structure will be at least more variable, exaggerated or repeatable in young than in old individuals (Prediction 2). Conversely, due to relative higher cognitive demands, social play unpredictability is expected to peak later and persist longer during the ontogeny. We expect old individuals' social play structure to be more variable, exaggerated or repeatable than young individuals' (Prediction 3).

Concerning the ontogeny of object play and functional manipulation in the genus, our hypothesis is a 'Higher unpredictability of object play among young individuals' (Hypothesis 2). In capuchin monkeys, younger individuals, usually engage in more extensive manipulative repertoire and unpredictability during object play than older individuals (Resende & Ottoni, 2002; Resende et al., 2014). The latter, more experienced with objects and with higher manipulatory skills, gradually extinguish the repertoire of non-functional manipulation and retain only the functional manipulation (i.e. foraging; Resende & Ottoni, 2002; Resende et al., 2014). We expect at least variability, exaggeration or repeatability to be higher in young individuals' object play sequences (Prediction 4). Also, object play repertoire should be larger in young individuals than in old individuals (Prediction 5).

Methods

Study site and study group

This study was carried at the campus of State University of Londrina, municipality of Londrina, Paraná, Brazil. This is an urban area with 20-hectares of semideciduous Atlantic Forest (23°19'45.2"S 51°12'25.8"W) connected to a riparian vegetation matrix, and small forest patches distributed among buildings and open areas (Figure 1).

We studied a fully habituated group of wild black-horned capuchin monkeys (*Sapajus nigritus*) that have inhabited the area at least since 1991, according to a documentary about the group produced by Vlamir J. Rocha (personal archive). The group has been studied since 2016 when identification of individuals was initiated. The group spent most of the time travelling and foraging in the small forest patches and the 20-hectare forest but also visited human buildings and fed on trash cans and human food. When foraging, individuals have not been observed using any kind of percussive, probe or digging tool so far. The monkeys were habituated to human presence, but we have observed occasional agonistic displays by capuchins to human visitors.

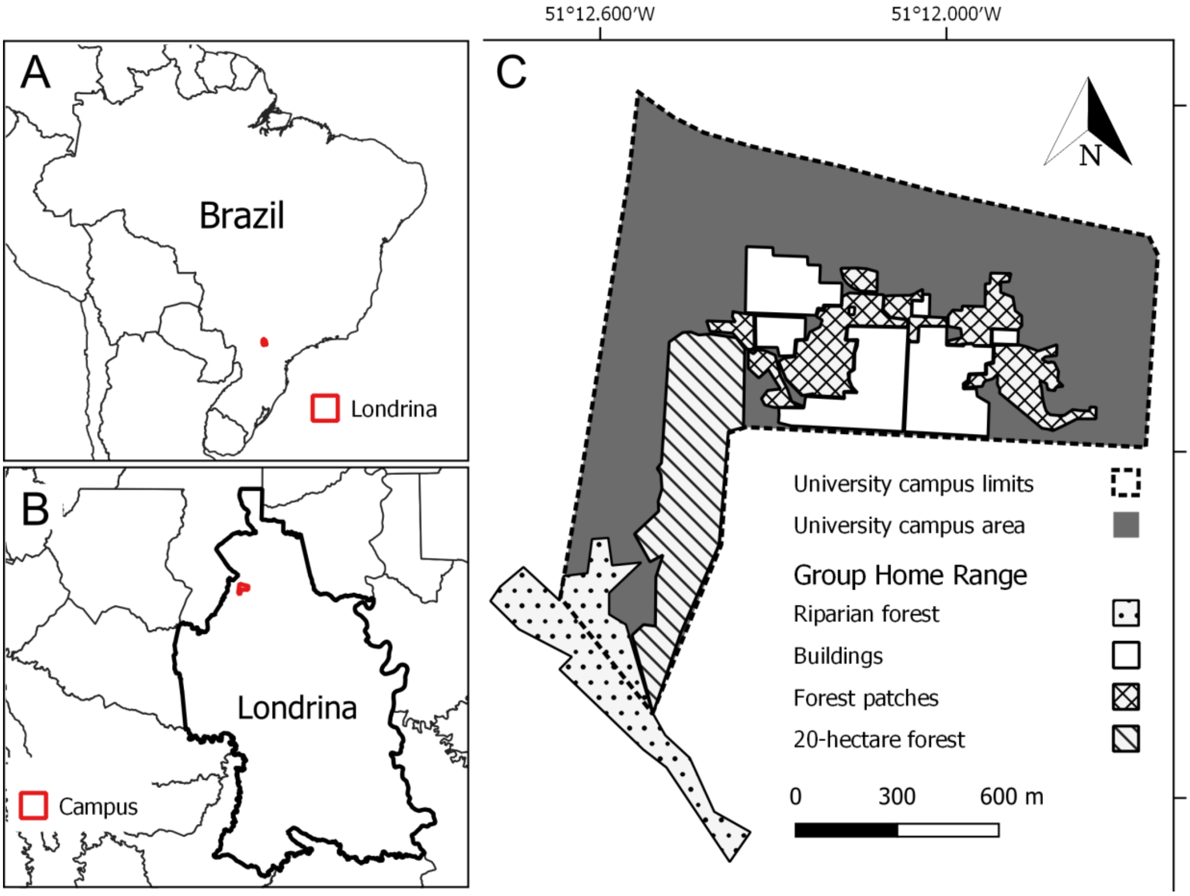

Figure 1. Map of the study area showing the home range of *Sapajus nigritus* within the campus of State University of Londrina, Londrina, Paraná state, Brazil and the neighboring riparian forest. A = Brazil and Londrina in South America, B = University campus in Londrina municipality and C = State University of Londrina campus areas and group home range.

The group ranged from 25 individuals in the beginning of data collection in July 2019 (Two adult males, eight adult females, eight juveniles and seven infants) to 35 individuals in the end of data collection in April 2021 (One adult male, two sub-adult males, nine females, 16 juveniles and seven infants). Individuals were classified in infant (0 to 1 year old), juvenile (1 to 4/5 years old), sub-adult (males: 5 to 6 years old) and adult (5/6 years old) age classes. Infants were divided in infant 1 (0 to 6 months old) and infant 2 (6 months to 1 year old) and juveniles were divided in juvenile 1, 2, 3 and 4 (Table 1; Resende, 2004). Harry, an adult male disappeared in June 2020, and we believe that he emigrated. An unknown male, Tom, immigrated into the group in June 2020 and, as his body and behavior were similar to Billy, we considered him to be in the same age class (Table 1).

Table 1. Group composition of *Sapajus nigritus* during the period of July 2019 to April 2021. The mothers of unidentified infants are indicated in parentheses. Infant 1: zero to six months old; Infant 2: six months to one year old; Juvenile 1 (Juv. 1): one to two years old; Juvenile 2 (Juv. 2): two years to three years old; Juvenile 3 (Juv. 3): three years to four years old; Juvenile 4 (Juv. 4): four to five years old; Sub-adult male (SubA): five to six years old; Adult male (Adult): six years old or more; Adult female: from five years old or from conception.

Name	**Sex**	**2019**	**2020-21**
Alfa - alpha male	Male	Adult	Adult
Harry	Male	Adult	Adult
Brown	Female	Adult	Adult
Dixie	Female	Adult	Adult
Jolie	Female	Adult	Adult
Juca	Female	Adult	Adult
Zee	Female	Adult	Adult
Zoey	Female	Adult	Adult
Piper	Female	Adult	Adult
Bailey	Female	Adult	Adult
Lucas	Female	Juv. 3	Adult
Billy	Male	Juv. 3	Juv. 4-subA/A
Tom	Male	-	Juv. 4-subA/A
Rob	Female	Juv. 2	Juv. 3-4
Oz	Undetermined	Juv. 2	Juv. 3-4
Goo	Undetermined	Juv. 2	Juv. 3-4
Feio	Female	Juv. 2	Juv. 3-4
Sol	Male	Juv. 1	Juv. 2-3
Alt	Female	Juv. 1	Juv. 2-3
Pirita	Undetermined	Infant 2	Juv. 1-2
Visa	Undetermined	Infant 2	Juv. 1-2
Nero	Undetermined	Infant 2	Juv. 1-2
Uatu	Undetermined	Infant 2	Juv. 1-2
Maul	Undetermined	Infant 2	Juv. 1-2
Pitt	Undetermined	Infant 2	Juv. 1-2
Drop	Undetermined	Infant 2	Juv. 1-2
Hex	Undetermined	-	Infant - Juv. 1
Choco	Undetermined	-	Infant - Juv. 1
Schino	Undetermined	-	Infant - Juv. 1
Infant (Bailey)	Undetermined	-	Infant 1
Infant (Brown)	Undetermined	-	Infant 1
Infant (Dixie)	Undetermined	-	Infant 1
Infant (Jolie)	Undetermined	-	Infant 1
Infant (Juca)	Undetermined	-	Infant 1
Infant (Zee)	Undetermined	-	Infant 1
Infant (Zoey)	Undetermined	-	Infant 1

Data collection

Preliminary observations of the study group were conducted from April to December 2018. During this time, we habituated the group, identified the individuals and created the ethogram of play behaviors through *ad libitum* observations (Altmann, 1974). Play behavior sequence data was collected by a single observer (EAF) for 65 days between 0900 h and 1700 h, from July 2019 and April 2021. Due to the COVID-19 (SARS-CoV-2) pandemic, fieldwork was interrupted from March 10, 2020 to October 25, 2020. EAF continued the fieldwork after the State University of Londrina authorized graduate students to resume activities. EAF conducted the fieldwork with one more researcher, FSMP, that conducted his own observations of the group. Both continuously wore face masks and kept social distancing. It was particularly important to keep wearing face masks to prevent any virus transmission to the observed primates.

The social group was followed by the observer, who alternated focus across subgroups of individuals. We conducted sequence sampling (Altmann, 1974) of visible play events. These events included fight, locomotor-rotational, object and social play. L-R play consisted of locomotor-rotational and self-directed play behaviors. Object play sequences consisted of locomotor-rotational behaviors with objects (e.g. gripping an object with hands or mouth) or object-directed play. Social play consisted of other-directed actions, socio-sexual behavior and displays. Fight play consisted of other-directed intense contact patterns and continuous exchange of blows between interactants. General play consisted of the succession of play categories: L-R, object, social and fight play, in an event. Categories, and play behaviors and displays observed in each category of play were defined from *ad libitum* observations of occurrences and based on ethograms for *Sapajus* (Table 2; Fragaszy et al., 2004; Lutz & Judge, 2017).

When an individual was observed in solitary play (L-R and object play sequences), we started recording the behavioral sequence in video. We interrupted the recording if the monkey engaged in other non-play activities for more than one minute (e.g. foraging, agonistic, traveling) or if we were unable to tell the continuity of play or the category of play due to loss of visual contact with the individual. The nearest individual observed playing was then sampled in the same manner. When an individual engaged in group play (social or fight play), we recorded all playing animals until the bout was over and then kept sampling the behavioral sequence of the first individual. If the sequence recording already started with a group play bout, we then sampled the visible individuals that kept playing in the same place after the bout end.

Table 2. Behaviors observed during play behavior for *Sapajus nigritus,* the type of sequence it is observed and the coding for the ‘T-pattern detection and analysis’.

Behavior	Sequence type	Description	*Theme* coding
Fight play	General	‘A’ engages in intense body contact with ‘B’, and have continuous exchange of blows.	A,b,fig A,e,fig
Locomotor-Rotational play	General	‘A’ moves in the environment with acrobatic and exaggerated movements. These are dissociated from foraging.	A,b,loc A,e,loc
Object play	General	‘A’ manipulates objects (branches, twigs, leaves, anthropic objects and edibles). Edibles like seeds, leaves and fruit are not eaten or manipulated in a foraging manner.	A,b,obj A,e,obj
Social play	General	‘A’ engages in coordinated play with one or more individuals. Sociosexual behavior during play is also included in this category. Intense body contact (Fight play) is not included in Social Play, but individuals may exchange less intense corporal contact patterns.	A,b,soc A,e,soc
Approach	L-R, object and social	While walking or galloping, ‘A’ approaches a walking or stationary ‘B’ from the distance of one meter.	A,b,approach,B
Beat	Object	‘A’ repeatedly hits an object with hands or feet.	A,b,beat,hand A,b,beat,feet
Beat with object	Object	‘A’ repeatedly holds an object and hits it against a surface with hands or feet.	A,b,beatw,hand A,b,beatw,feet

Bipedalism	L-R, object and social	'A' stands on an assisted or free bipedal posture while stationary or walking.	A,b,bipedalism,idle A,b,bipedalism,walking
Chase	Social	'A' runs after 'B', as 'B' runs away.	A,b,chase,B A,b,chased,B
Climb	L-R, object and social	'A' climbs a vertical structure, natural or anthropic.	A,b,climb
Drop another	Social	'A' hangs onto or pushes a hanging 'B', 'B' falls from the suspensory position. 'A' might fall.	A,b,drop,B
Embrace	Social	Dorso-ventral contact between two individuals when there is no thrusting movements.	A,b,embrace
Eyebrow raising	Social	'A' rises eyebrows and scalp, while looking at 'B'. Sometimes 'A' would eyebrow raise for no specific interactor (e.g. mounts).	A,b,raise A,b,raise,B
Fall	L-R, object and social	'A' fall or drops from a vegetal or human structure.	A,b,fall
Flee	Social	'A' quickly back off from 'B', interrupting the bout.	A,b,flee,B
Gallop	L-R, object and social	'A' runs or run in an exaggerated manner.	A,b,gallop
Grab/pull	Social	'A' grabs and/or pull 'B' head, arms, legs, torso, tail or the fur on those areas.	A,b,grab,head,B A,b,grab,arms,B A,b,grab,legs,B A,b,grab,torso,B A,b,grab,tail,B
Grin	Social	'A' retracts the mouth corners, baring the teeth. Sometimes 'A' would grin for no specific interactor (e.g. mounts).	A,b,grin A,b,grin,B
Hang	L-R, object and social	'A' adopts a suspensory position with hand (h), hands (hs), foot (fo), feet (fe), tail (t). Modifiers are the combination of the limbs used in suspension.	A,b,hang,fht A,b,hang,fohst A,b,hang,h A,b,hang,..
Hang on another	Social	'A' hangs onto 'B'.	A,b,hangot,B
Head tilting	Social	'A' tilts head rhythmically sideways and/or frontwards while looking at 'B'.	A,b,htilt,B
Hide	Social	'A' stands behind a structure quickly hiding and reappearing in the field of view of 'B'.	A,b,hide,B
Jump backwards	L-R and social	'A' leaps away from 'B'.	A,b,jback,B
Jump over	L-R and social	'A' leaps over the body of 'B', they might touch.	A,b,jover,B
Jump towards/lunge	Social	'A' leaps in the direction of 'B'.	A,b,jtow,B

Lay	L-R, object and social	'A' lies down ventrally, laterally or dorsally. 'A' might approach and lie down in front of another individual.	A,b,lay A,b,lay,B
Leap	L-R, object and social	'A' throws the body forward using limb propulsion. 'A' might leap and fall in the same location (s) or leap in order to achieve a further location (ac).	A,b,leap,s A,b,leap,ac
Line - Social	Social	'A' chases one or more individuals around a structure or object.	A,b,line,B,C
Line - Solitary	L-R and social	'A' walk or run around a structure or object.	A,b,linesol
Look between legs - Social	Social	'A' looks through own legs in a bipedal or quadrupedal motion going towards 'B'. 'A' might touch 'B'.	A,b,lblsoc,B
Look between legs - Solitary	L-R	'A' looks through his legs while stationary or in a bipedal or quadrupedal motion.	A,b,lbl
Manipulate	L-R and object	'A' touches, spins and passes an object from limb to limb using hands, feet and/or tail.	A,b,manipulate,hand A,b,manipulate,feet A,b,manipulate,handfeet A,b,manipulate,tail
Mount	Social	Dorso-ventral contact between two individuals when there are thrusting movements. This behavior is durational, starts (b) with the mounting and ends with dismounting (e).	A,b,mount,B A,e,mount,B A,b,mounted,B A,e,mounted,B
Mouth	Social	'A' touches 'B' head, arms, legs, torso, tail or the fur on those areas with mouth, lips or teeth.	A,b,mouth,head,B A,b,mouth,arms,B A,b,mouth,legs,B A,b,mouth,torso,B A,b,mouth,tail,B
Mouth object	Object	'A' touches an object with lips, tongue and/or teeth.	A,b,mouthobj
Move away	L-R and Social	'A' walks or gallops more than one meter away from another individual/individuals.	A,b,away,B,C
Nuzzle	Social	'A' softly touches 'B' with mouth and nose.	A,b,nuzzle,B
Open mouth threat display	Social	'A' widely opens mouth and jaws and bare teeth. 'A' may have piloerection and raise eyebrows.	A,b,omtd,B
Overlord	Social	'A' and 'B' assume a dorso-ventral or lateral embrace posture while threatening 'C' during play.	A,b,overlord,B.

Penile or genital display/chest rubbing	Social	'A' spreads legs with a penile erection and/or gently rubs hands on the chest while looking at 'B'. Sometimes 'A' would chest rub for no specific interactor (e.g. after mounts).	A,b,penile,B
Play with water - Social	Social	'A' plays with one or more individuals in a water pond, bathing, drinking water and throwing water on the interactants.	A,b,watersoc,B,C
Play with water - Solitary	Object	'A' plays with one or more individuals in a water pond, bathing, drinking water and throwing water out of the pond and onto self.	A,b,water
Poke	Social	'A' softly and quickly touches 'B' with a hand. Commonly observed when 'B' is not playing.	A,b,poke,B
Push	Object	'A' applies pressure horizontally to an object using hands and/or feet causing it to move.	A,b,push,hand A,b,push,feet A,b,push,handfeet
Relaxed open mouth	Social	Relaxed facial expression with a wide opened mouth. Also known as play face.	A,b,rom
Roll	L-R and social	On a substrate 'A' rotates on a head-feet or left-right axis.	A,b,roll
Rub	Object	'A' holds and rubs an object against a surface, applying pressure vertically on the object with hands or feet.	A,b,rub,hand A,b,rub,feet
Self-manipulation	L-R, object and social	'A' manipulates its own body touching limbs with hands feet and/or mouthing limbs (mouth).	A,b,automan A,b,automan,mouth
Shred	Object	'A' rips apart an object with hands or feet.	A,b,shred,hand A,b,shred,feet
Slide	L-R and social	'A' moves without propulsion along a surface in contact with limbs or stomach. A might slide while adopting a suspensory posture.	A,b,slide
Somersault	L-R and social	'A' rotates the body on a head-feet axis while leaping or falling.	A,b,somer
Spin	L-R and social	'A' rotates on own axis on a quadrupedal motion.	A,b,spin
Stare	Social	'A' fixedly looks at 'B' for more than two seconds. May be accompanied by facial displays.	A,b,stare,B

Swing	L-R and social	While hanging 'A' moves the body back and forth or in a circular fashion.	A,b,swing
Tackle	Social	'A' jumps on 'B' making body contact.	A,b,tackle,B
Top another	Social	'A' moves up to 'B', assuming a quadrupedal posture, clinging or lying over 'B'.	A,b,top,B
Top object	Object	'A' moves up to an mobile object.	A,b,topobj
Vocalization	L-R and social	'A' vocalizes during play.	A,b,vocal
Walk	L-R, object and social	'A' moves in a relaxed and slow pace.	A,b,walk

During the recordings we noted the identity and age class of the individuals, and confirmed it during video data coding. Uncertain age class identifications and sequences with low visibility of behavioral sequences were excluded from analyses (777s of total play). For the comparison of play structure on the ontogeny, infant 2, juveniles 1 and 2 were grouped as young individuals and juveniles 3 and 4 were grouped as old individuals.

Data coding

EAF coded behavioral sequences, individual age class and identities on videos with the *Behavioral Observation Research Interactive Software, BORIS* (Friard & Gamba, 2016). We coded four types of sequences: general, L-R, object and social (non-fighting) play. A single video contained an individual alternating between L-R, object, social and fight play, and non-play (locomotion or idle) instances. General play sequences consisted of alternating L-R, object, social and fight play categories, and non-play. Each category was coded at the starting and ending second. Each category was coded if presented exclusive behaviors for at least two seconds. Non-exclusive behaviors required the continuity of the sequence in order to code the type of play the animal engaged. For example, two seconds of *Chase* another individual code social play, however, behaviors such as *Leap* and *Jump Over* occurred in L-R and social contexts and would be coded according to the concurrent and proceeding context: coding L-R if the individual was playing solitary and social play if interacting with another. If the individual walked or remained idle for two seconds without subsequent play behaviors, this time was not coded until engaging in any category of play. L-R, object and social play sequences were coded by occurrence, second by second (s-s) for subjects; fight play sequences were not coded and analyzed in this study. During social play sequences, individuals would interact with many individuals and swiftly change between age-matched and mismatched interactors. Also, in social play, individuals were not measuring strength by exchanging blows, and because of that our approach on social non-fight play did not consider the identity and age class of interactants. For all types of sequences, we coded subjects independently and if we were able to identify the individual age-class and behavioral sequence in the video. L-R, object and social play sequences required great visibility resulting in shorter well-coded sequences (about 5-90 s).

In order to analyze the temporal structure of sequences across age classes with the TPA, we sampled sequences for each type of sequence and age class. For consistent comparisons of quantitative data obtained from the TPA, the number of time points (seconds) in samples and the number of samples for different groups (young and old individuals) were standardized (Casarrubea et al., 2015; Magnusson, Burgoon & Casarrubea, 2016). General samples were shortened to a 60 s duration while L-R and social samples were shortened to 15 s, and object samples were shortened to 10 s. The number of samples was balanced for each individual in each age class and samples were performed at least one minute apart. For sample independency, we first sampled from the beginning of sequences from different years for each individual and unidentified individuals, then different months, then different days, then different sequences in the same day, then behaviors performed at least one minute apart in the same sequence (Table 3).

Table 3. Number of samples for each individual and unidentified individuals in general, L-R, object and social play sequences. The number of samples for young individuals (0.5 to 3 years old) is in regular typography and for old individuals (3 to 5 years old) is in bold.

Individual	General (N = 18)	L-R (N = 14)	Object (N = 10)	Social (N = 23)
Billy	**8**	**5**	**5**	**16**
Choco	2	1	1	-
Feio	2, **1**	1, **2**	**1**	4
Goo	**3**	1, **4**	**1**	**6**
Unidentified	1	7	4	7
Maul	4	-	3	2
Oz	1, **1**	1, **1**	-	2
Pirita	3	-	-	1
Rob	1, **1**	**1**	**2**	3
Schino	-	-	-	2
Sol	2, **2**	3, **1**	2	2
Tom	**2**	-	**1**	**1**
Uatu	1	-	-	-
Visa	1	-	-	-

Data analyses

In order to assess the temporal structure and detect temporal behavior patterns in general, L-R, object and social play across age classes, the standardized samples were transposed to event log files, consisting of behaviors occurring at specific time points (seconds). These log files were inputted to the *Theme* software (PatternVision Ltd, Iceland). In *Theme* we executed a multivariate analysis called T-pattern detection and analysis (TPA), that identifies recurring series of behavioral elements (T-patterns) in and across samples. We executed the TPA for each type of sequence for each age class, performing a concatenated-sample TPA. In the concatenated-sample TPA, samples are grouped in a single log-file, allowing the algorithm to detect T-patterns across samples. The quantitative data: variability, exaggeration and repeatability were obtained from each sample for statistical comparison between young and old individuals.

The TPA is a powerful algorithm for discovering the nonobvious or hidden sequences and temporal patterns of behavior (Magnusson, 2016). Across samples, the algorithm initially searches for pairs of behaviors that form T-patterns consisting of two elements (i.e. behaviors). These are pairs for which behavior B (e.g. Gallop) occurs after A (e.g. Walk) in a certain time window more often than expected by chance. If this is the case, a first level T-pattern, consisting of two elements (length = 2), is detected and represented as [A,b,walk A,b,gallop]. From this first level T-pattern, behaviors and other T-patterns are tested in time windows in order to detect longer and statistically significant T-patterns (e.g. [[A,b,walk A,b,gallop] A,b,fall]]; [[A,b,walk A,b,gallop] [A,b,leap,ac A,b,fall]]). More behaviors and T-patterns are tested in several time windows until there are no longer T-patterns for which there are statistically significant critical intervals for subsequent behaviors or patterns (Magnusson, 2016). In order to investigate the structural variability across age classes we compared the following T-pattern parameters: variability, exaggeration and repeatability. Variability is defined as the number of different detected T-patterns in a sample. Exaggeration is the number of behaviors that form T-patterns, or the length of each detected T-pattern in a sample. Repeatability is the number of occurrences of each detected T-pattern in a sample (Cenni et al., 2020; Gunst et al., 2020). To perform the concatenated-sample TPA, we defined these standard search parameters for general, L-R and object play sequences: significance level of 0.005, minimum T-pattern occurrences: 2, lumping factor of 0.90, shuffling randomization, and 10 randomization runs. For social play sequences a lumping factor of 0.8 was applied due to no T-patterns detected with lumping factor 0.9. Further description, details, and experimental approaches on the T-pattern detection and analysis can be found in Casarrubea et al. (2015) and Magnusson, Burgoon & Casarrubea (2016).

In order to compare the manipulation repertoire young and old individuals we built a rarefaction curve of behaviors observed during object play sequences for each age class. For the rarefaction curve, we conducted the ‘Mao tau’ analytical procedure in Paleontological Statistics (PAST) version 3.21 (Hammer, Harper & Ryan, 2001) with 95% confidence level. For this analysis, each ten seconds of coded object play sequences was considered as one sampling unit, 56 sampling units for young individuals and 21 sampling units for old individuals. Rarefaction curves of observed behaviors can be used to verify the completeness of behavioral repertoires and to compare repertoires with same operational definitions (Dias et al., 2009).

Statistical Analyses

T-patterns are detected with a high level of statistical significance, however, the high amount of possible combinations in behavioral sequences brings into question whether T-patterns are detected only by chance. To deal with this issue, *Theme* applies a Monte Carlo approach by repeatedly shuffling each occurring series and displaying the mean and standard deviation for randomized patterns of each length (Casarrubea et al., 2015; Magnusson, 2016). The mean number of T-patterns (±SD) detected in randomized data is compared to the real number of T-patterns detected.

We compared the number of different T-patterns (variability), the length of T-patterns detected (exaggeration) and the occurrence of T-patterns (repeatability) of general ($N = 18$), L-R ($N = 14$), object ($N = 10$) and social ($N = 23$) play sequences between young individuals and old individuals with Mann-Whitney U tests ($\alpha = 0.05$).

Ethical note

This research was noninvasive and observational only. The black-horned capuchin monkey study group was habituated to human presence and to the researchers. This study complied with the legal and ethical requirements of Brazil and the project was previously approved by the Animal Ethics Committee of the State University of Londrina (CEUA n. 12803.2016-74). The authors declare no conflict of interests.

Data availability

The data analyzed during the current study are available from the corresponding author on reasonable request.

Results

We followed the group for 94 h and 45 min, and recorded 2 h and 26 min of play behavior sequences, summing 0.03 of the total observation time. We coded 1050 s of L-R, 560 s of object and 1020 s of social play sequences for young individuals and 410 s of L-R, 210 s of object and 850 s of social play sequences for old individuals. We searched for T-patterns in general, L-R, object and social play sequences for young and old individuals. After randomizing and re-analyzing the sequences we found significant differences between the total number of T-patterns in real and randomized data for all types of sequences and for T-patterns of all lengths (Figure 2).

The number of unique T-patterns detected (i.e. variability) was similar for young and old individuals in L-R, object and social play sequences (2(interquartile range (IQR): 1.75-3.75) and 2(IQR: 2-4), Mann-Whitney U test: N = 14, U = 101.5, P = 0.8862; 1.5(IQR: 1-3.5) and 1(IQR: 1-1), Mann-Whitney U test: N = 10, U = 63.5, P = 0.2671; 2(IQR: 1-2) and 2(IQR: 1-3), Mann-Whitney U test: N = 23, U = 236, P = 0.5165; Figure 3). A higher median for variability was observed in general sequences for old individuals, however, this variation was diminished by a higher interquartile range in the variability of young individuals, and this difference was not statistically significant (6(IQR: 1-9.5) and 4(IQR: 1.25-10.75), Mann-Whitney U test: N = 18, U = 174, P = 0.7103; Figure 3).

We found statistically significant differences in the length of T-patterns (i.e. exaggeration) among age classes in general and L-R sequences. Despite similar medians, T-patterns in older individuals' general sequences were more likely to be longer than T-patterns in younger individuals' general sequences (3(IQR: 2-5) and 3(IQR: 2-4), Mann-Whitney U test: N = 18, U = 6053, P = 0.0019; Figure 4). While young individuals L-R sequences were more exaggerated than old individuals' sequences (2(IQR: 2-3) and 2(IQR: 2-2), Mann-Whitney U test: N = 14, U = 951, P = 0.009026; Figure 4), Object and Social sequences exaggeration did not differ for age classes (2(IQR: 2-3) and 2(IQR: 2-3), Mann-Whitney U test: N = 10, U = 383, P = 0.7134; 2(IQR: 2-2) and 2(IQR: 2-2), Mann-Whitney U test: N = 23, U = 1260, P = 0.8881; Figure 4).

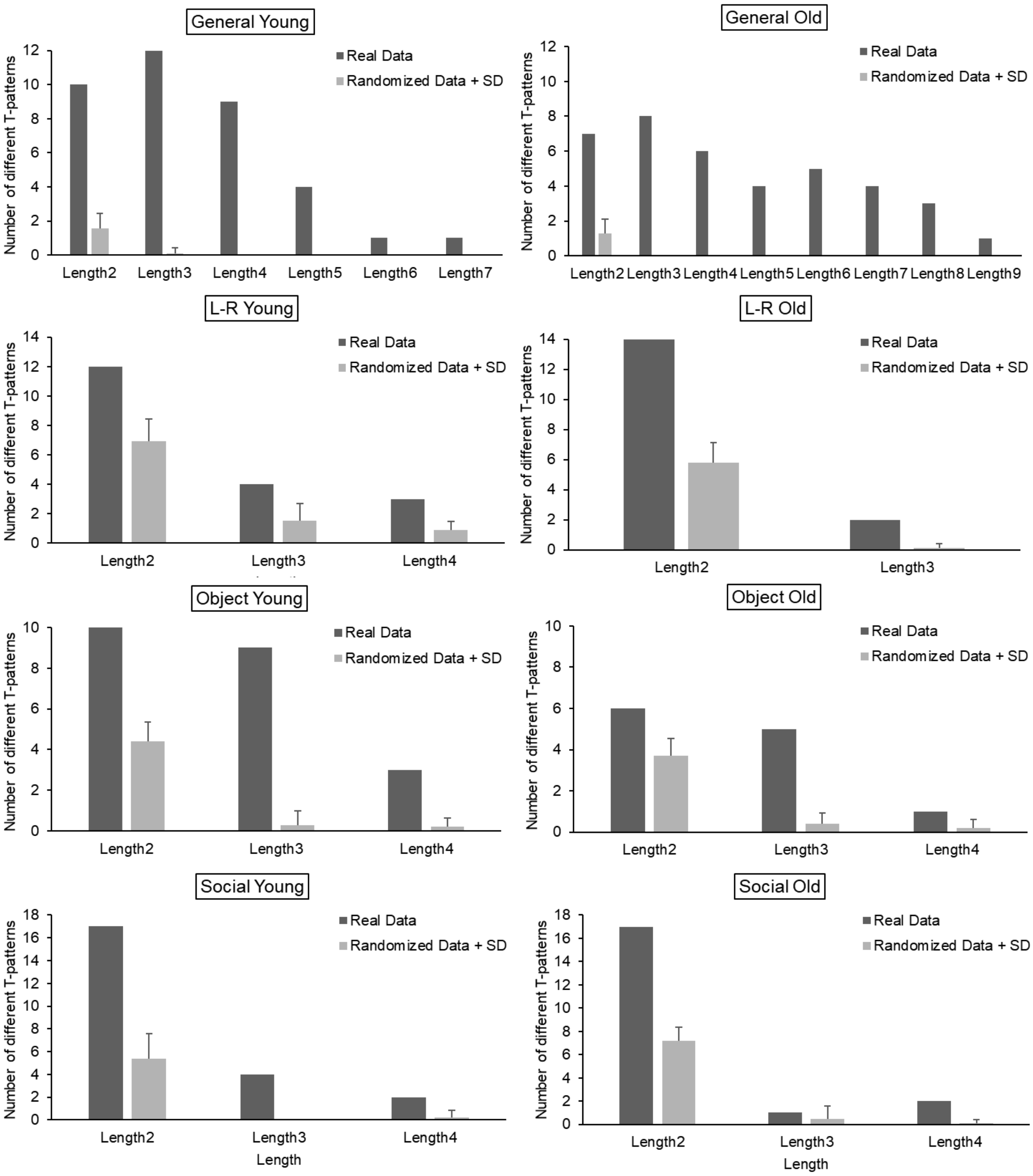

Figure 2. Number of different T-patterns of various lengths in real data (dark bars) and randomized data (light bars). Data from general (N= 18), locomotor-rotational (N = 14), object (N = 10) and social play (N = 23) sequences of young (0.5 to 3 years old) and old individuals (3 to 5 years old).

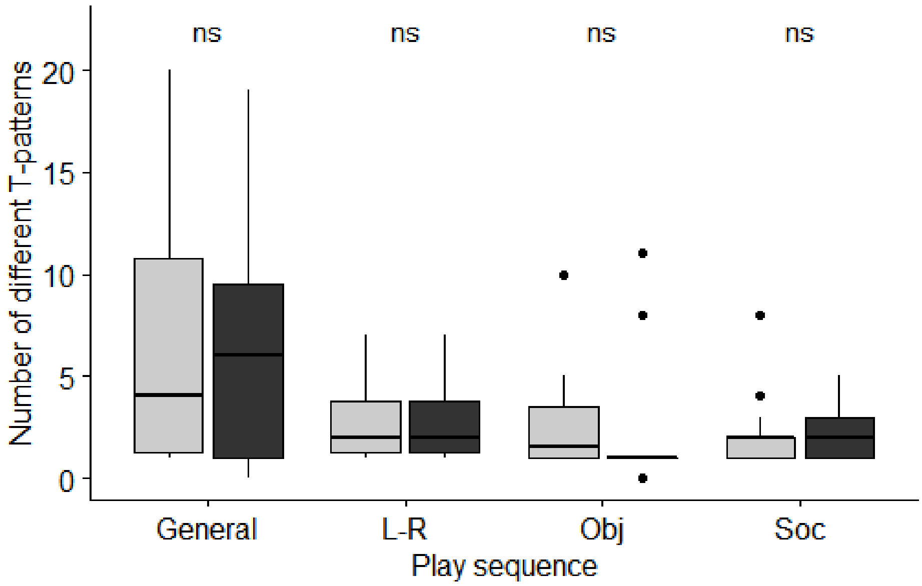

Figure 3. Boxplot (median, range, interquartile range and outliers) for the number of different T-patterns found across general (General), locomotor-rotational (L-R), object (Obj) and social play (Soc) sequences for young (light boxplots, 0.5 to 3 years old) and old individuals (dark boxplots, 3 to 5 years old). ns: non-significant, P > 0.05.

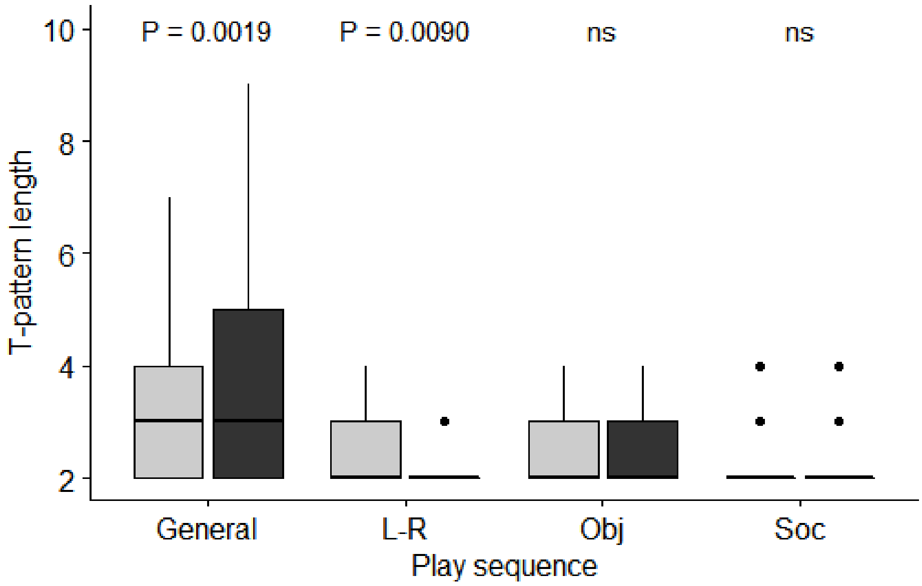

Figure 4. Boxplot (median, range, interquartile range and outliers) for the length of T-patterns (i.e. number of elements of each T-pattern) found across general (General), locomotor-rotational (L-R), object (Obj) and social play (Soc) sequences for young (light boxplots, 0.5 to 3 years old) and old individuals (dark boxplots, 3 to 5 years old). ns: non-significant, P > 0.05.

T-patterns in young individuals' sequences generally occurred more times (i.e. more repeatable) than in old individuals' sequences. We found that repeatability was significantly higher for young than old individuals in general, L-R and object play sequences (1(IQR: 1-1.25) and 1(IQR: 1-1), Mann-Whitney U test: N = 18, U = 8601, P = 0.02914; 4(IQR: 2-9) and 2(IQR: 1-4.75), Mann-Whitney U test: N = 14, U = 1113.5, P = 0.0009; 5(IQR: 3-9) and 4(IQR: 2-5), Mann-Whitney U test: N = 10, U = 490.5, P = 0.0265; Figure 5). No significant difference was found in repeatability for social sequences among age classes (3(IQR: 1-5.5) and 3(IQR:1-6), Mann-Whitney U test: N = 23, U = 1238, P = 0.9467; Figure 5).

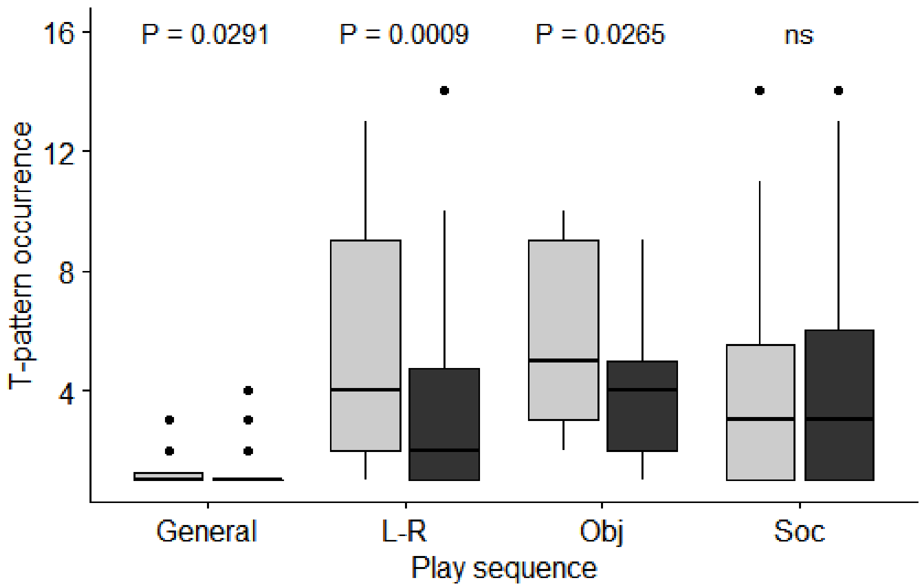

Figure 5. Boxplot (median, range, interquartile range and outliers) for the occurrence of T-patterns (i.e. number of occurrences of each T-pattern in a sequence) found across general (General), locomotor-rotational (L-R), object (Obj) and social play (Soc) sequences for young (light boxplots, 0.5 to 3 years old) and old individuals (dark boxplots, 3 to 5 years old). ns: non-significant, P > 0.05.

During object play sequences, young individuals engaged in 14 types of object manipulation while old individuals engaged in seven types of manipulation. Rub with hands, manipulate with tail, top object, beat object with hands, shred object with hands or feet, and push object with hand and feet were patterns exclusive to object play in young individuals. There was a faster increase of the manipulation repertoire in young individuals in comparison to old individuals (Figure 7). At the total sampled time for older individuals (210 s), young individuals accumulated 11.1 ± 1.7 unique manipulation behaviors while old individuals accumulated 7 ± 1.6 behaviors.

Table 4. Manipulation behaviors observed during object play for young (0.5 to 3 years old) and old individuals (3 to 5 years old). Behaviors are listed according to the overall frequency and repertoire size is presented in parenthesis. Behavior descriptions are displayed on Table 2 (above) and underlined behaviors were observed exclusively for the age class in the category.

Age Class	Manipulation behaviors
Young	manipulate,hand; mouthobj; water; rub,hand; push,hand; manipulate,handfeet; beatw,hand; shred,hand; manipulate,tail; topobj; beat,hand; manipulate,feet; shred,feet; push,handfeet (14).
Old	water; manipulate,hand; mouthobj; manipulate,handfeet; beat,hand; push,hand; manipulate,feet (7).

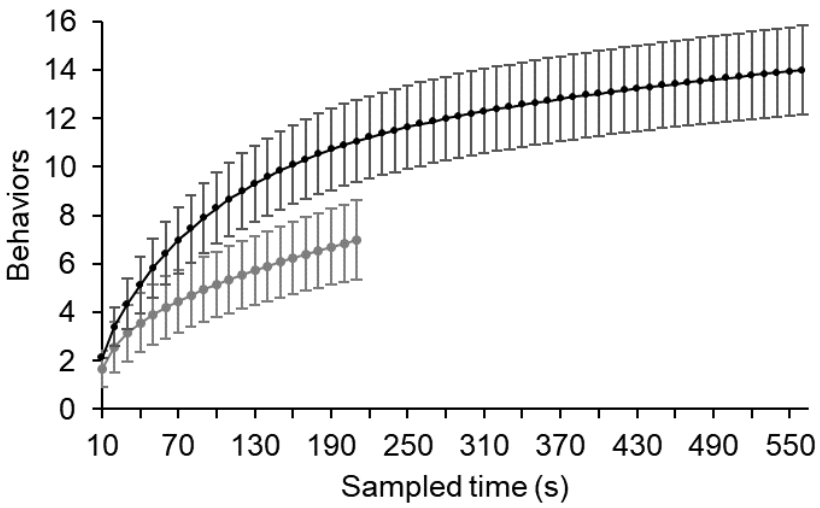

Figure 6. Behavior accumulation curves and standard deviation bars for manipulation behaviors observed during object play for young (dark line, 0.5 to 3 years old) and old (light line, 3 to 5 years old) individuals.

As there were no significant differences between young and old individuals on social play unpredictability, and general play structure analysis was inconclusive, the ‘Training for the unexpected’ hypothesis was not fully supported. However, there were structural differences among the age classes that supported the prediction for L-R play structure. The ‘Higher unpredictability of object play among young individuals’ hypothesis was supported, as object play was more repeatable in younger individuals and this age class presented more types of object manipulation (Table 5).

Table 5. Predictions for the ‘Training for the unexpected’ hypothesis (H1) and ‘Higher unpredictability of object play among young individuals’ (H2). YI = young individuals (0.5 to 3 years old), OI = old individuals (3 to 5 years old).

Hypotheses	Predictions	Expected			
		Variability	Exaggeration	Repeatability	
H1	1. General	YI = OI ✓	YI = OI ×	YI = OI ×	Inconclusive
	2. L-R	YI > OI ×	YI > OI ✓	YI > OI ✓	Supported
	3. Social	YI < OI ×	YI < OI ×	YI < OI ×	Not supported
H2	4. Object	YI > OI ×	YI > OI ×	YI > OI ✓	Supported
	5. Repertoire	Repertoire for object play YI > OI			Supported

Discussion

As black-horned capuchin monkeys develop, there is a change in play behavior structure. Young individuals were more exaggerated and repeatable in L-R play structure and repeatable in Object play structure. The data only supports Prediction 2, thus providing partial support for the ‘Training for the unexpected’ hypothesis, as younger individuals engaged in more self-handicapping during L-R play. However, social play unpredictability was conservative for age classes and we found no support for the Prediction 3, that older individuals engage in more unpredictable social play structure due to the high cognitive requirements of social play. Our second hypothesis, ‘Higher unpredictability of object play among young individuals’, was supported, both predictions 4 and 5 were true, younger individuals engaged in more repeatable sequences and more types of manipulation during object play.

There is a consistent difference in overall rate and play behavior between wild and captive capuchins. In captivity, play is observed when the group remains undisturbed, and juveniles engage in higher rates of play than in wild groups (*Sapajus* in captivity: Visalberghi & Guidi, 1998: 43,4%; Fragaszy et al., 2004: 21-24%; Paukner & Suomi, 2008: 9.2%). In natural environments, juveniles generally play when the group is stationary, and play rates are lower than in captivity (Wild *Cebus,* 3.45%: Fontaine, 1994; Fragaszy et al., 2004; Wild *Sapajus,* 1.6%: Wright et al., 2019). These rates are associated to the nutritional and travel demands of wild capuchins, resulting in less spare time for play and more time devoted to foraging and travelling (Visalberghi & Guidi, 1998; Paukner & Suomi, 2008). Even when actively searching for play behavior, this behavior consisted of only 3% of the total contact time with the group. This budget is more similar to the wild groups, even though they live in an urban area and have access to human provided food.

General play was more exaggerated in old individuals while young individuals presented shorter and more repeatable temporal patterns. General play sequences consist of changes between categories of play or interactants, and longer T-patterns (range: 2-9) would lead us to conclude that old individuals alternated more between motivational contexts than young individuals (range: 2-7). However, we found that despite shorter, T-patterns in young individuals' sequences were repeated more times in a 1-minute sequence. This leads to an inconclusive analysis as short structures of different motivational contexts being repeated more in a 1-minute sequence can be equally unpredictable to longer structures with less repetition in a 1-minute sequence. Prevalence in different categories during general play sequences may be unrelated to age but explained by a differential variation in sequences in an individual level that was not evaluated in this study. As evidenced for captive *Sapajus apella,* there was no significant differences for categories among ages (0.5-1 year and 1-4 years old) and there was a significant effect of subject on the distribution of time in categories *(*Lutz & Judge, 2017). Infant and juvenile capuchins join and leave bouts in quick succession, changing interactants and play types (Fragaszy et al., 2004). This pattern was observed in infants and juveniles up to 3 years old and here we evidence that there might be no definite contrast between young and old juveniles play changeability (Fragaszy et al., 2004).

Locomotor-rotational play was more exaggerated and repeatable among young individuals than old individuals. We can say that L-R structure is less constrained and more unpredictable in younger individuals. Therefore, older individuals, despite presenting certain level of unpredictability through engaging in various temporal structures, are more constrained in their L-R structure. As predicted by the 'Training for the unexpected' hypothesis, young individuals engaged in more self-handicapping through unpredictable and unconstrained sequences. In young individuals, self-handicapping during L-R play may be a form of creating and experiencing unexpected events on the environment. In these situations, physical and emotional capabilities can be developed to deal with unpredictable scenarios and behavioral sequences (Špinka et al., 2001). Old individuals would be self-handicapping less as they are more familiar to the environment and require less training of locomotor movements during play (Špinka et al., 2001). Young individuals of several species engage in intense handicapping movements in their play sequences, including leaps, dropping, climbing and extensive repertoire for suspensory positions (Fontaine, 1994; Wells & Turnquist, 2001; Workman & Covert, 2005; Bezanson, 2012). Oppositely, the postural repertoire, especially suspensory positions, of older individuals is reduced, and this decrease is strongly related to less time devoted to play and a more sedentary behavior (Dunbar & Badam, 1998; Wells & Turnquist, 2001; Workman & Covert, 2005; Bezanson, 2012). In this study, the variability of play did not differ among classes. However, we showed that there is a reduction in the randomness of the L-R play structure in capuchin older individuals.

We expected old individuals to peak in social play unpredictability. However, social play structure was conservative across immature capuchin development. Though unpredictability during L-R play is a cognitively demanding activity, the nature of social play is characterized by a higher unpredictability and cognitive demand as the animal is performing based on partner movements, sequences, mental states and strength (Špinka et al., 2001). Young and old individuals showed the same complexity of social play, therefore, the cognitive demands for non-fight social play are either not highly demanding as fight play or developed in an early age. The second alternative is corroborated for *Sapajus* as the full repertoire for play fights has been shown to develop early in ontogeny and juveniles of all ages engaged in play from lowest to the highest levels of fight intensity (Lutz & Judge, 2017). However, some species may have a delayed peak for social play as evidenced for *Pan troglodytes* and *P. paniscus*. In the species, social play rate is similar among infants (0.5-4 years old) and juveniles (4-7 years old) but complexity of sequences (i.e. the number of unique behaviors in a sequence) in fight play is more complex in juvenile dyads (Cordoni & Palagi, 2011). We showed that there is no ontogenetic peak for social play unpredictability. The tendency to engage in social play unconstrained sequences is similar among young and old individuals when the effect of the interactor or sequence of interactors is not evaluated.

Our second hypothesis, 'Higher unpredictability of object play among young individuals', was fully supported. Object play was more repeatable in young individuals, suggesting a higher level of unpredictability. In a *Sapajus* sp. semi-free group in southeastern Brazil, older individuals were less variable in sequences for cracking nuts while younger individuals presented less efficient sequences and used more strikes to open a nut, what can be related to a higher repeatability (Resende et al., 2014). In wild coastal-foraging *Macaca fascicularis,* older individuals also engaged in more optimal sequences for cracking oysters and unattached food (Tan, 2017). When comparing a functional usage for stone handling in free-ranging urban *Macaca fascicularis* with the general stone handling, a form of play/exploratory manipulation in the species, non-functional manipulation showed more exaggerated and more repeatable T-patterns (Cenni et al., 2020). This examples show that individuals that are more experienced with manipulation present more constrained sequences in functional tool usage and that object manipulation/exploration is more unconstrained than functional manipulation. From our study we conclude that these differences are not a clear cut when only non-functional behavior structure, such as object play, is taken in account.

Throughout development, *Sapajus* juveniles engage in differential categories of manipulative behavior. From simple manipulation: picking, biting, licking, hitting, handling, poking and rubbing objects, individuals engage in further levels of combinatorial manipulation (Resende et al., 2008). Combinatorial manipulation levels range from bringing an object to contact with a surface to the sequential manipulations of two objects and use of objects as a foraging tool through banging stones at nuts on a substrate (Resende et al., 2008). Here, manipulation observed during object play was restricted to simple manipulation and up to the first level of combinatorial manipulation. The first level of combinatorial manipulation was observed in the group during foraging activities. Individuals in the group stroke *Joannesia princeps* Vell. and *Castanea sativa* Mill. fruits against tree trunks and roofs of buildings in order to break/open the fruit shell and ingest seeds. Object manipulation complexity in older individuals, therefore, may be performed during functional object manipulation. We conclude that, in this group, the categories of manipulative behavior observed during play are the same used in functional manipulation. Elsewhere, *Sapajus* groups with tool use traditions present manifold uses for stone and stick as tools and engage in more complex levels of object play and functional manipulation (Resende & Ottoni, 2002; Resende et al., 2008; Falótico & Ottoni, 2016; Falótico et al., 2018). In those groups, social learning is important for the acquisition of combinatorial levels of manipulation, and in young individuals, foraging object manipulation is interspersed with object play (Coelho et al., 2015; Falótico, Bueno & Ottoni, 2021). Accordingly, foraging manners and tool traditions in a group may influence the extent of manipulation repertoire during play behavior and play repertoire may assemble the functional repertoire due to the observation of functional manipulation in older individuals from infancy.

Studying play behavior in wild primates is a challenging task. Play behavior is scarce and recording sequences of this fast and unpredictable behavior in natural environment may be uneasy. A tool for identifying and analyzing temporal patterns in small samples, while retaining statistical power, is the TPA. We showed here that structure of play behavior changes during the ontogeny of wild capuchin monkeys. Contrary to some of our predictions, this structure change does not appear to be in accord to the ‘Training for the unexpected’, however, regarding manipulation behaviors, the change does appear to be related to learning of functional behaviors used for foraging. Play structure is an important component for an accurate comprehension of the functions of play in primates, and efforts in this sense are essential.

References

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour,* 49 (3-4), 227-267. https://www.jstor.org/stable/4533591.

Bekoff, M. (1988). Motor Training and Physical Fitness: Possible Short- and Long-Term Influences on the Development of Individuals Differences in Behavior. *Developmental Psychobiology*, 21, 6. https://doi.org/10.1002/dev.420210610.

Bezanson, M. (2012). The Ontogeny of Prehensile-Tail Use in *Cebus capucinus* and *Alouatta palliata*. *American Journal of Primatology* 00, 1-13. https://doi.org/10.1002/ajp.22028.

Bezerra, B.M., Barnett, A.A., Souto, A., & Jones, G. (2011). Ethogram and Natural History of Golden-backed Uakaris (*Cacajao melanocephalus*). *International Journal of Primatology*, 32, 46-68. https://doi.org/10.1007/s10764-010-9435-1.

Birnie, A.K., Hendricks, S.E., Smith, A.S., Milam, R., & French J.A. (2012). Maternal gestational androgens are associated with decreased juvenile play in white-faced marmosets (*Callithrix geoffroyi*). *Hormones and Behavior*, 62, 136-145. https://doi.org/10.1016/j.yhbeh.2012.05.014.

Bramblett, C.A. (1978). Sex differences in the acquisition of play among juvenile Vervet Monkeys. In Smith, E.O. (Ed.), Social Play in Primates (pp. 33-48). New York: Academic Press.

Burghardt, G.M. (1998). The evolutionary origins of play revisited: lessons from turtles. In Bekoff, M. & Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative and Ecological Perspectives (pp. 1-26). Cambridge: Cambridge University Press.

Burghardt, G.M. (2005). The Genesis of Animal Play: Testing the Limits. Cambridge, Massachussets: The MIT Press.

Byers, J.A. (1998). Biological effects of locomotor play: getting into shape, or something more specific? In Bekoff, M. & Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative and Ecological Perspectives (pp. 205-220). Cambridge: Cambridge University Press.

Candland, D.K., French, J.A., & Johnson, C.N. (1978). Object-play: test of a categorized model by the genesis of object-play in *Macaca fuscata*. In Smith, E.O. (Ed.), Social Play in Primates (pp. 259-296). New York: Academic Press.

Casarrubea, M., Jonsson, G.K., Faulisi, F., Sorbera, F., Di Giovanni, G., Benigno, A., Crescimanno, G., & Magnusson, M.S. (2015). T-pattern analysis for the study of temporal structure of animal and human behavior: A comprehensive review. *Journal of Neuroscience Methods*, 239, 34-46. https://doi.org/10.1016/j.jneumeth.2014.09.024.

Casarrubea, M., Faulisi, F., Cudia, A., Cancemi, D., Cardaci, M., Magnusson, M.S., & Crescimanno, G. (2017). Discovery of recurring behavioural sequences in Wistar rat social activity: Possible support to studies on Autism Spectrum Disorders. *Neuroscience Letters*, 653, 58-63. https://doi.org/10.1016/j.neulet.2017.05.031.

Cenni, C., Casarrubea, M., Gunst, N., Vasey, P.L., Pellis, S.M., Wandia, I.N., & Leca, J. (2020). Inferring functional patterns of tool use behavior from the temporal structure of object play sequences in a non-human primate species. *Physiology & Behavior*, 222, 112938. https://doi.org/10.1016/j.physbeh.2020.112938

Chalmers, N.R. (1980). The ontogeny of play in feral Olive Baboons (*Papio Anubis*). *Animal Behavior*, 28, 570-585. https://doi.org/10.1016/S0003-3472(80)80066-2.

Coelho, C.G., Falótico, T., Izar, P., Mannu, M., Resende, B.D., Siqueira, J.O., & Ottoni, E.B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, 18, 911-919. https://doi.org/10.1007/s10071-015-0861-5.

Cordoni, G. & Palagi, E. (2011). Ontogenetic Trajectories of Chimpanzee Social Play Similarities with Humans. *PLoS ONE*., 6, 11. https://doi.org/10.1371/journal.pone.0027344.

De Boer, R.A., Overduin-de-Vries, A.M., Louwerse, A.T., & Sterck, E.H.M. (2013). The Behavioral Context of Visual Displays in Common Marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 75, 1084-1095. https://doi.org/10.1002/ajp.22167.

Dias, P.A.D., Rangel-Negrín, A., Coyohua-Fuentes, A., & Canales-Espinosa, D. (2009). Behaviour accumulation curves: a method to study the completeness of behavioural repertoires. *Animal Behaviour*, 77, 1551-1553. https://doi.org/ 0.1016/j.anbehav.2009.02.015.

Dunbar, D.C. & Badam, G.L. (1998). Development of Posture and Locomotion in Free-ranging Primates. *Neuroscience and Behavioral Reviews*, 22, 4, 541-546. https://doi.org/10.1016/s0149-7634(97)00042-0.

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Fragaszy, D. (2016). When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, 19. 605-618. https://doi.org/10.1007/s10071-016-0965-6.

Fagen, R. (1981). Animal Play Behavior. Oxford: Oxford University Press.

Falótico, T. & Ottoni, E.B. (2016). The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour*, 153, 4, 421-442. https://doi.org/10.1163/1568539X-00003357.

Falótico, T., Coutinho, P.H.M., Bueno, C.Q., Rufo, H.P. & Ottoni, E.B. (2018). Stone tool use by wild capuchin monkeys (*Sapajus libidinosus*) at Serra das Confusões National Park, Brazil. *Primates*, 59, 385-394. https://doi.org/10.1007/s10329-018-0660-0.

Falótico, T., Bueno, C.Q., & Ottoni, E.B. (2021). Ontogeny and Sex differences in object manipulation and probe tool use by wild tufted capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, 83, 5. https://doi.org/10.1002/ajp.23251.

Fontaine, R. (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., Visalberghi, E., & Fedigan, L.M. (2004). The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge: Cambridge University Press.

Friard, O. & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *British Ecological Society*, 7, 11, 1325-1330. https://doi.org/10.1111/2041-210X.12584.

Govindarajulu, P., Hunte, W., Vermeer, L.A., & Horrocks, J.A. The Ontogeny of Social Play in a Feral Troop of Vervet Monkeys (*Cercopithecus arthiops sabaeus*): The Function of Early Play. *International Journal of Primatology*, 14, 5, 701-719. https://doi.org/10.1007/BF02192187.

Graham, K.L. & Bughardt, G.M. (2010). Current perspectives on the Biological Study of Play: Signs of Progress. *The Quarterly Review of Biology*, 85, 4, 393-418. https://doi.org/10.1086/656903.

Gray, P. (2019). Evolutionary Functions of Play: Practice, Resilience, Innovation and Cooperation. In Smith, P.K. & Roopnarine, J.L. (Eds.), The Cambridge Handbook of Play, Developmental and Disciplinary Perspectives (pp. 84-102). Cambridge: Cambridge University Press.

Gunst, N., Casarrubea, M., Vasey, & P.L., Leca, J. (2020). Is female-male mounting functional? An analysis of the temporal of sexual behaviors in Japanese macaques. *Physiology and Behavior*, 223, 112983. https://doi.org/10.1016/j.physbeh.2020.112983.

Hammer, Ø., Harper, D.A.T., & Ryan, P.D. (2001). Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4,1. https://palaeo-electronica.org/2001_1/past/issue1_01.htm

Heldstab, S.A., Isler, K., Schuppli, C., & van Schaik, C.P. (2020). When ontogeny recapitulates phylogeny: Fixed neurodevelopmental sequences of manipulative skills among primates. *Science advances*, 6, 30, eabb4685. https://doi.org/ 10.1126/sciadv.abb4685.

Koops, K., Furuichi, T., Hashimoto, C. & van Schaik, C.P. (2015). Sex Differences in Object Manipulation in Wild Immature Chimpanzees (*Pan troglodytes schweinfurthii*) and Bonobos (*Pan paniscus*): Preparation for Tool Use? *PLoS ONE*, 10, 10, e0139909. https://doi.org/10.1371/journal.pone.0139909.

Lutz, M.C. & Judge, P.G. (2017). Self-handicapping during play fighting in capuchin monkeys (*Cebus apella*). *Behaviour*, 154, 9-10, 909-938. https://doi.org/10.1163/1568539X-00003449.

Magnusson, M.S. (2016). Time and Self-Similar Structure in Behavior and Interactions: From Sequences to Symmetry and Fractals. In Magnusson, M.S., Burgoon, J.K., Casarrubea, M. (Eds.), Discovering Hidden Temporal Patterns in Behavior and Interaction: T-Pattern Detection and Analysis with THEME™ (pp. 3-36). New York: Humana Press.

Magnusson, M.S., Burgoon, J.K., & Casarrubea, M. (2016). Discovering Hidden Temporal Patterns in Behavior and Interaction: T-Pattern Detection and Analysis with THEME™. New York: Humana Press.

Martin, P. & Caro, T.M. (1985). On the Functions of Play and Its Role in Behavioral Development. *Advances in the Study of Behavior*, 15, 59-103. https://doi.org/10.1016/S0065-3454(08)60487-8.

Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of Social Play in Juvenile Lowland Gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology*, 49, 4, 433-445. https://doi.org/10.1002/dev.20219.

Palagi, E. (2010). Playing at Every Age: Modalities and Potential Functions in Non-Human Primates. In Nathan, P. & Pellegrini, A.D. (Eds.), The Oxford Handbook of the Development of Play. https://doi.org/10.1093/oxfordhb/9780195393002.013.0007.

Paukner, A., & Suomi, S.J. (2008). Sex differences in play behavior in juvenile tufted capuchin monkeys (*Cebus apella*). *Primates*, 49, 288-291. https://doi.org/10.1007/s10329-008-0095-0.

Pellegrini, A.D., Dupuis, D., & Smith, P.K. (2007). Play in evolution and development. *Developmental review*, 27, 261-276. https://doi.org/10.1016/j.dr.2006.09.001.

Pellegrini, A.D. (2010). The Development and Function of Locomotor Play. In Nathan, P. & Pellegrini, D. (Eds.), The Oxford Handbook of Play. Oxford: Oxford University Press. https://doi.org/10.1093/oxfordhb/9780195393002.013.0014.

Pellis, S.M. & Pellis, V.C. (1997). Targets, Tactics, and the Open Mouth Face During Play Fighting in Three Species of Primates. *Aggressive Behavior*, 23, 41-57. https://doi.org/10.1002/(SICI)1098-2337(1997)23:1<41::AID-AB5>3.0.CO;2-W.

Pellis, S.M. & Iwaniuk, A.N. (2000). Adult-Adult Play in Primates: Comparative Analyses of Its Origin, Distribution and Evolution. *Ethology*, 106, 1083-1104. https://doi.org/10.1046/j.1439-0310.2000.00627.x.

Pellis, S.M. (2002). Sex Differences in Play Fighting Revisited: Traditional and Nontraditional Mechanisms of Sexual Differentiation in Rats. *Archives of Sexual Behavior*, 31, 1. https://doi.org/ 10.1023/a:1014070916047.

Pellis, S.M. & Pellis, V.C. (2011). To Whom the Play Signal Is Directed: A Study of Headshaking in Black-Handed Spider Monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology*, 125, 1. https://doi.org/ 10.1037/a0020547.

Pellis, S.M., Burghardt, G.M., Palagi, E., & Mangel, M. (2015). Modeling play: distinguishing between origins and current functions. *Adaptive Behavior*, 23, 6, 331-339. https://doi.org/10.1177/1059712315596053.

Perry, S.E., Barrett, B.J., & Godoy, I. (2017). Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 30, 7806-7813. https://doi.org/10.1073/pnas.1620739114.

Petrů M., Špinka, M., Charvátová, V., & Lhota, S. (2009). Revisiting Play Elements and Self-Handicapping in Play: A Comparative Ethogram of Five Old World Monkey Species. *Journal of Comparative Psychology*, 123, 3, 250-263. https://doi.org/10.1037/a0016217.

Resende, B.D. & Ottoni, E.B. (2002). Brincadeira e aprendizagem do uso de ferramentas em macacos-prego (*Cebus apella*). *Estudos de Psicologia*, 7, 1, 173-180. https://doi.org/10.1590/S1413-294X2002000100018.

Resende, B.D. (2004). Ontogenia de comportamentos manipulativos em um grupo de macacos-prego (*Cebus apella*) em situação de semiliberdade [Doctoral thesis, University of São Paulo]. USP Digital Library. https://doi.org/10.11606/T.47.2004.tde-03062008-140907.

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.

Resende, B.D., Nagy-Reis, M.B., Lacerda, F.N., Pagnotta, M & Savalli, C. (2014). Tufted capuchin monkeys (*Sapajus* sp) learning how to crack nuts: Does variability decline throughout development? *Behavioural Processes*, 109, 89-94. https://doi.org/10.1016/j.beproc.2014.09.002.

Rosenblum, L.A. & Cooper, R.W. (1968). The Squirrel Monkey. New York: Academic Press, Inc.

Rowel, T.E. & Chism, J. (1986). The Ontogeny of Sex Differences in the Behavior of Patas Monkeys. *International Journal of Primatology*, 7, 1, 83-107. https://doi.org/10.1007/BF02692310.

Špinka, M., Newberry, R.C., & Bekoff, M. (2001). Mammalian play: Training for the Unexpected. *The Quartely Review of Biology*, 76, 2, 141-168. https://doi.org/ 10.1086/393866.

Tan, A.W.Y. (2017). From Play to Proficiency: The Ontogeny of Stone-Tool Use in Coastal-Foraging Long-Tailed Macaques (*Macaca fascicularis*) From a Comparative Perspection-Action Perspective. *Journal of Comparative Psychology*, 131, 2. https://doi.org/10.1037/com0000068.

Visalberghi, E. & Guidi, C. (1998). Play Behaviour in Young Tufted Capuchin Monkeys. *Folia Primatologica*, 69, 419-422. https://doi.org/10.1159/000021665.

Wells, J.P. & Turnquist, J.E. (2001). Ontogeny of Locomotion in Rhesus Macaques (*Macaca mulatta*): II. Postural and Locomotor Behavior and Habitat Use in a Free-Ranging Colony. *American Journal of Physical Anthropology*, 115, 80-94. https://doi.org/10.1002/ajpa.1059.

Workman, C., & Covert, H.H. (2005). Learning the Ropes: The Ontogeny of Locomotion in Red-Shanked Douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh Langurs (*Trachypithecus hatinhensis*) I. Positional Behavior. *American Journal of Physical Anthropology*. https://doi.org/10.1002/ajpa.20205.

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, e23067. https://doi.org/10.1002/ajp.23067.

5 CONCLUSÃO

Estudar o comportamento de brincadeira em primatas de vida livre pode ser desafiador. Apesar de facilmente reconhecível, é um comportamento de baixa frequência, que acontece de forma rápida e imprevisível, o que dificulta a amostragem das sequências comportamentais. A análise '*T-pattern detection and analysis*' é uma ferramenta para identificar e analisar padrões temporais em amostragens pequenas com alto poder estatístico. A estrutura da brincadeira se altera durante a ontogenia de macacos-prego de vida livre. Ao contrário de algumas predições, essa alteração da estrutura não parece estar de acordo com a hipótese 'Treinando para o inesperado'. Em relação ao comportamento manipulativo, no entanto, a alteração da estrutura da brincadeira parece se relacionar com o aprendizado de manipulação funcional e de seu uso durante o forrageio. A estrutura da brincadeira é um componente importante para uma compreensão acurada da função da brincadeira em primatas e esforços nesse sentido do conhecimento são essenciais.