ALEXANDRE DE JESUS RODRIGUES MALTA

O EFEITO DA COMPOSIÇÃO DO GRUPO NO DESENVOLVIMENTO MOTOR DE INFANTES DE UM PRIMATA DE REPRODUÇÃO COOPERATIVA: O PAPEL DO GÊNERO

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade da Universidade Federal Rural de Pernambuco (PPGBio-UFRPE), como pré-requisito para obtenção do título de mestre em Biodiversidade.

Orientadora: Profa. Dra. Nicola Schiel

Coorientação: Dra. Christini Caselli

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SUMÁRIO

RESUMO

O tamanho e a composição dos grupos sociais podem moldar padrões comportamentais e a estrutura das relações dos animais que compõem esses grupos. Uma das principais vantagens de se viver em grupos sociais é a possibilidade de algumas espécies desenvolverem o cuidado com a prole ou *reprodução cooperativa*, comportamento este muito comum em primatas. Pesquisas envolvendo o cuidado com a prole já tem sido realizadas de forma extensiva, no entanto, pouco se sabe quais seriam as consequências que o número de indivíduos em um grupo pode exercer no desenvolvimento motor dos infantes. Especificamente em se tratando do sagui-comum (*Callithrix jacchus*), um pequeno primata Neotropical, estes caracterizam-se pelo seu peculiar sistema social em que indivíduos não-reprodutores, auxiliam no cuidado da prole de forma cooperativa. Diante disso, procuramos aferir o efeito da composição do grupo no desenvolvimento motor de seus infantes. Mais especificamente, procuramos averiguar a relação de ajudantes no desenvolvimento motor dos infantes. Para tanto, foram acompanhados quatro grupos de sagui comum em vida livre, em uma área de Mata Atlântica de Pernambuco, nordeste do Brasil. O comportamento motor de infantes com idades de um a quatro meses foram registrados. Utilizamos como indicador de desenvolvimento motor o índice de diversidade motora (Shannon Index). Através deste verificamos que o índice de diversidade motora de infantes com dois meses de idades se mostrou de forma prematura em grupos com menos adultos. Em grupos com mais fêmeas a diversidade de infantes com dois meses de idade revelou ser significativamente menor quando comparada aos infantes com três meses de idade. Contudo, a diversidade motora aumenta com a idade independentemente do número de machos adultos no grupo. Estes resultados trazem um novo viés em relação ao papel das fêmeas nestes pequenos primatas. Enquanto machos têm um importante papel no cuidado com a prole, as fêmeas parecem ter um papel chave no desenvolvimento motor dos infantes. No sistema de reprodução desses animais, aparentemente, a ausência de ajudantes reflete em um desenvolvimento motor prematuro por parte dos infantes.

Palavras-chave: grupo social; cooperação; infantes; *Callithrix jacchus*

ABSTRACT

The size and composition of social groups can shape behavioral patterns and the structure of relationships of the animals that make up these groups. One of the main advantages of living in social groups is the possibility for some species to develop offspring care or cooperative reproduction, a behavior that is very common in primates. Researches involving the care of offspring have already been carried out extensively, however, little is known about the consequences that the number of individuals in a group can exert on the motor development of infants. Common marmoset (*Callithrix jacchus*), a small Neotropical primate, are characterized by a peculiar social system in which non-breeding individuals help in the care of the offspring in a cooperative way. In view of this, we sought to assess the effect of group composition on the motor development of their infants. More specifically, we seek to investigate the relationship of helpers in the motor development of infants. For this purpose, four groups of free-living common marmosets were monitored in an area of the Atlantic Forest in Pernambuco, northeastern Brazil. The motor behaviors of infants aged one to four months were recorded. We used the motor diversity index (Shannon Index) as an indicator of motor development. Through this we verified that the index of motor diversity of infants with two months of age revealed to be prematurely in groups with fewer adults. In groups with more females, the diversity of two-month-old infants was significantly lower when compared to three-month-old infants. However, motor diversity increases with age regardless of the number of adult males in the group. These results bring a new bias in relation to the role of females in these small primates. While males play an important role in caring for the offspring, females seem to play a key role in the infants' motor development. In the reproduction system of these animals, apparently, the absence of helpers reflects in a premature motor development regarding the infants.

Key-words: social group; cooperation; infants; *Callithrix jacchus*

FUNDAMENTAÇÃO TEÓRICA

Vida em Grupo

O tamanho e a composição dos grupos sociais podem moldar padrões comportamentais e a estrutura das relações dos animais que compõem esses grupos (SILK, 2007). Adicionalmente, a aptidão de um indivíduo quanto aos comportamentos coletivos e cooperativos nos grupos de animais sociais, podem definir como os indivíduos reservam tempo e espaço (MARKHAM et al., 2015). Segundo a teoria da seleção de grupos os atributos coletivos, se não forem moderadamente controlados, podem ocasionar a deterioração do próprio grupo (ALCOCK, 2011). Quando em grupos sociais, a integridade do grupo depende de os indivíduos concordarem que certas regras regulam seu comportamento (BEKOFF, 2001), ou seja, a organização social produz seus próprios benefícios na adaptação do indivíduo e da espécie em relação ao ambiente, mas ela também pode exercer pressão sobre o indivíduo (MAJOLO; HUANG, 2018).

São poucas as espécies que conseguem se organizar em sociedades como, por exemplo, os leões, considerados os únicos felinos que formam sociedades (MOSSER; PACKER, 2009). Os leões mantêm um grupo coeso formado principalmente por fêmeas e jovens e, geralmente, há um macho adulto que auxilia o grupo na defesa contra outros machos nômades podendo estes, formar coalizões (NOWAK, 2005). Os elefantes, por sua vez, exibem associações ao longo do tempo, demonstrando um comportamento afiliativo sendo altamente cooperativos na defesa do grupo, aquisição de recursos, cuidado com os filhotes e tomada de decisões (POOLE; MOSS, 2008). Alguns outros animais apresentam uma formação social tão complexa que são chamados de *eusociais.* Nestes sistemas, os integrantes do grupo possuem uma divisão de trabalho, cuidado cooperativo com a prole e também há sobreposição de gerações como, por exemplo, os cupins, abelhas e ratos-toupeiras (RICKLEFS; RELYEA, 2016; KAPPELER, 2019).

Nesse contexto, diversos estudos enfatizam que a vida em grupo pode trazer custos como também benefícios a depender das condições ecológicas sob as quais cada espécie vive (RICKLEFS; RELYEA, 2016). A defesa contra predadores é um exemplo de como os animais se adaptam para sobreviver. Ao formar grupos, os animais podem se tornar mais visíveis a predadores e com isso precisam trabalhar juntos de forma *ativa*, quando todos agem coletivamente para se defenderem ou *passiva*, quando um indivíduo usa o grupo para se esconder ou confundir o predador (RUBENSTEIN; ALCOCK,

2019). Por outro lado, a vida em grupo pode trazer alguns efeitos negativos aos indivíduos como, por exemplo, riscos de transmissão por doenças e parasitas, uma vez que em populações muito densa pode aumentar as chances de uma doença se espalhar e levar a epidemias. (RICKLEFS; RELYEA, 2016). Ao se estabelecer uma hierarquia, em alguns grupos sociais, pode haver uma supressão de indivíduos subordinados limitando a sua reprodução (CLUTTON-BROCK, 2016). Da mesma forma como pode ocorrer competição reprodutiva por parceiros para se acasalar (RUBENSTEIN; ALCOCK, 2019), e também por posição hierárquica (BROOM; KOENIG; BORRIES, 2009). Estes conflitos por sua vez podem levar a morte de infantes (ALCOCK, 2011) e até mesmo canibalismo (FOUILLOUX; RINGLER; ROJAS, 2019). Há também efeitos negativos que podem surgir, concomitante, pelas vantagens do comportamento social, ou seja, grandes grupos conseguem recursos alimentares com mais facilidade, porém caso a quantidade disponível seja limitada pode ser um problema na hora de compartilhar o alimento entre membros do grupo o que pode levar a conflitos (RICKLEFS; RELYEA, 2016).

Uma das principais vantagens de se viver em grupos sociais é a possibilidade de algumas espécies desenvolverem o cuidado com a prole ou *reprodução cooperativa*, comportamento este muito comum em primatas (ALCOCK, 2011; BSHARY, 2010; CLUTTON-BROCK, 2006; DUGATKIN, 2014; MARKHAM; GESQUIERE, 2017; SILK, 2007; RICKLEFS; RELYEA, 2016).

Cuidado com a prole

De acordo com Kappeler (2019) o cuidado com a prole é considerado um dos principais pilares de um sistema social. Este se caracteriza por interações sociais, comunicação e hierarquia de dominância, fornecendo assim a base para o estudo sistemático da complexidade social. O surgimento do cuidado parental é incerto, porém desperta interesse desde as observações de Darwin a respeito da seleção natural (KLUG; ALONZO; BONSALL, 2012), pois este tipo de comportamento foi crucial para algumas espécies de mamíferos perpetuarem suas linhagens, desenvolvendo os mais diversos mecanismos de proteger sua prole, com participação não apenas dos próprios genitores (parental) como também de outros indivíduos do grupo (aloparental) (ALONZO; KLUG, 2012; RYMER; PILLAY, 2018).

O apego entre progenitores e filhotes é importante para animais cujas crias precisam de cuidados parentais para seu desenvolvimento (SAITO; IZUMI;

NAKAMURA, 2011). Como qualquer repertório comportamental, o cuidado parental despende energia (TARDIF; HARRISON; SIMEK, 1993), não só para quem gera e amamenta, como também para os cuidadores, que ficarão co-responsáveis pelo desenvolvimento motor e cognitivo do recém-nascido durante boa parte de seu ciclo de vida (ISLER; VAN SCHAIK, 2012; MARKHAM; GESQUIERE, 2017; SMISETH; KÖLLIKER; ROYLE, 2012).

Em mamíferos, intervenção dos machos no cuidado com a prole ocorre em aproximadamente 10% dos gêneros (KLEIMAN; MALCOLM, 1981), cujas ações podem ser classificadas de duas formas: *direta* - quando o macho do grupo oferece ajuda diretamente aos filhotes que pode influenciar no seu desenvolvimento físico e na sua sobrevivência, como por ex. carregar, alimentar e brincar; *indireta* –quando o macho influencia na sobrevivência do infante, por exemplo, atuando na defesa do território e proteção da fêmea (KLEIMAN; MALCOLM, 1981).

Diante dos desafios de viver em grupo, o cuidado com a prole surge como mais uma estratégia de sobrevivência entre mamíferos sociais, principalmente primatas e seu estudo possibilita acompanhar o desenvolvimento dos infantes, principalmente buscar entender o efeito do grupo no desenvolvimento motor dos infantes que ainda é desconhecido.

Desenvolvimento motor

De acordo com Newell (1986) desenvolvimento motor é um processo de mudança nos movimentos relacionados com a idade, bem como de interações das características do próprio indivíduo no ambiente que o cerca e das tarefas a serem executadas. O desenvolvimento nos mamíferos passa por várias etapas e sofre influência de diversos fatores, seja em vida livre (LEA et al., 2015) ou até mesmo em cativeiro (LEWIS, 2005; VENTURA; BUCHANAN-SMITH, 2003), em que podem interferir por exemplo na sua qualidade de vida, na reprodução, comportamento e coordenação motora (AUSDERAU et al., 2017; LEA et al., 2015; LINDSTRÖM, 1999; YANG et al., 2015). Especificamente em se tratando de primatas, estes apresentam longos períodos de desenvolvimento e, logo após o nascimento, os infantes são expostos à manipulação de co-específicos, incluindo pais, cuidadores e pares socialmente dominantes (JONES, 2005).

Segundo Bădescu et al. (2016) dentro das populações, fatores específicos, como risco de infanticídio, predação e competição por alimento podem impactar nas taxas de

desenvolvimento de filhotes em termos de crescimento e tempo para alcançar a independência nutricional. A independência nutricional começa quando, após a fase de amamentação, as mães ainda permitem que os filhotes fiquem por perto, para observar o que comer e como obter alimentos, evitar que outros indivíduos tentem roubar o alimento de seu filhote e, principalmente, promover o desenvolvimento das habilidades nos infantes (NICOLSON, 1987).

Nicolson (1987) descreve sobre a independência locomotora, em que o infante, após o nascimento, será carregado não só pela mãe como também por outros membros do grupo durante um período de sua vida, e depois será forçado a locomover-se por si só. Esse autor salienta que este incentivo parte principalmente de sua genitora, mas a decisão da fêmea em recusar ajudar o filhote dependerá das habilidades desenvolvidas pelo infante bem como suas decisões na alternância de ajudantes.

Callithrix jacchus

Callithrix jacchus também conhecido como sagui-comum, sauim, soim ou mico-estrela é uma espécie de primata neotropical. São primatas neotropicais de pequeno porte possuindo uma coloração em sua maior parte cinza claro a castanho e preto, uma cauda longa, apresentando alternadamente anéis claros e escuros. A face apresenta uma mancha branca e tufos com pelos brancos que circundam a orelha (ARAÚJO et al., 2000). Possuem unhas em forma de garras, 32 dentes com incisivos inferiores alongados e estreitos adaptados para extrair exsudados (BERTASSOLI et al. 2013).

São primatas endêmicos do nordeste brasileiro, distribuindo-se originalmente na porção norte do Rio São Francisco, pelos estados de Alagoas, Pernambuco, Paraíba, Rio Grande do Norte, Ceará, Piauí, Maranhão e Bahia (MORAES et al., 2019; RYLANDS; COIMBRA-FILHO; MITTERMEIER, 2009).Contudo, em decorrência de introduções, estes primatas podem ser encontrados em outras regiões, além de sua distribuição original, como no estado de Sergipe (ALBUQUERQUE et al., 2014), Rio de Janeiro (RUIZ-MIRANDA et al., 2006), São Paulo (BRAZ et al., 2019), Paraná (GONZALES; MAGALHÃES JÚNIOR, 2016), Minas Gerais (SILVA et al., 2018), Santa Catarina (NUNES, 2006) e até mesmo na Argentina (RYLANDS; COIMBRA-FILHO; MITTERMEIER, 2009). Uma das consequências como espécie introduzida é a competição por recursos com espécies nativas, principalmente as ameaçadas de extinção como mico-leão-dourado (*Leontopithecus rosalia*) (RUIZ-MIRANDA et al., 2006) bem

como podem ocorrer hibridizações com outras espécies de *Callithrix* (e.g. *C. penicilatta*) (MALUKIEWICZ, 2019).

Saguis-comuns ocupam os mais diversos tipos de habitat que se encontram desde ambientes de Mata Atlântica e Caatinga (RYLANDS; COIMBRA-FILHO; MITTERMEIER, 2009; MORAES et al., 2019) até ambientes urbanos (ANDRADE, 2021). Segundo Schiel e Souto (2017) características morfológicas, fisiológicas e comportamentais podem ter levado ao sucesso ecológico dos saguis-comuns nos diversos tipos de habitat. Neste sentido, sua plasticidade comportamental e ecológica o fez sobreviver em ambientes com altas temperaturas e estresse hídrico, ao desenvolver estratégias para persistir em um ambiente semiárido como a Caatinga (DE LA FUENTE et al., 2014; ABREU et al., 2016; GARBER et al., 2019).

A dieta do sagui-comum é composta por vários itens disponíveis na natureza como: pequenos vertebrados, invertebrados, frutas, flores, néctar, sementes e exsudados das árvores (AMORA; BELTRÃO-MENDES; FERRARI, 2012; SCHIEL et al., 2010; SILVA et al., 2017; ABREU et al., 2016; SOUZA-ALVES; BARBOSA; HILÁRIO, 2020). Os saguis apresentam um padrão bimodal de exploração do exsudato, com picos pela manhã e ao final da tarde (PINHEIRO; MENDES PONTES, 2015). Os exsudatos contêm uma alta concentração de água, o que pode ser importante para estes animais que residem em ambientes semiárido como na Caatinga, especialmente durante a longa estação seca e principalmente para fêmeas que precisam amamentar gêmeos (GARBER et al., 2019). Estas cavidades abertas para extração da goma também podem ser marcadas com odor, principalmente pela parte anogenital (THOMPSON et al., 2018) e a partir destas marcações odoríferas é possível transmitir informações a respeito da situação reprodutiva, social (SMITH, 2006), bem como um melhor reconhecimento dos integrantes dos grupos envolvidos de forma a possibilitar futuros acasalamentos (LAZARO-PEREA, 2001).

Callithrix jacchus são predominantemente diurnos, despertam e saem para forragear nas primeiras horas da manhã, passando a maior parte de suas atividades diárias forrageando por alimentos, seja no alto das árvores, nos sub-bosques até mesmo no solo (DE LA FUENTE et al., 2014; PINHEIRO; MENDES PONTES, 2015; SCHIEL; SOUTO, 2017). Sua área de vida são as menores dentro deste gênero não alcançando 6,0 ha (PINHEIRO; MENDES PONTES, 2015; GARBER et al., 2019), uma vez que estas pequenas áreas de vida estariam relacionadas a densidade de árvores gomíferas (THOMPSON et al., 2013). Havendo sobreposição da área de vida entre

grupos sociais de *Callithrix*, comportamentos territoriais se apresentam de várias formas como: exibição de genitálias, piloereção, marcação de cheiro e raramente contato agonístico (LAZARO-PEREA, 2001).

O tamanho do grupo varia de 4-14 membros (ABREU et al., 2016), que podem ser compostos por indivíduos infantes, juvenis, subadultos e adultos (INGRAM, 1977; STEVENSON; RYLANDS 1988; MISSLER et al., 1992; CASTRO-LEÃO; DÓRIA NETO; SOUSA, 2009). O grupo apresenta uma hierarquia com um casal reprodutor dominante e outros indivíduos subordinados. Há fatores importantes relacionados à hierarquia entre fêmeas dominantes e subordinadas, em que estudos em cativeiro demonstraram que as dominantes podem provocar inibições da ovulação de fêmeas subordinadas (ABBOTT et al., 1981; BARRET; ABBOTT; GEORGE, 1990).Porém, em um estudo de campo, constatou-se que pode haver mais de uma fêmea reprodutora num mesmo grupo (RODA; MENDES PONTES, 1998), em que fêmeas subordinadas podem se acasalar com parceiros que imigraram (ARRUDA et al., 2005; LAZARO-PEREA, 2001; NIEVERGELT et al., 2000).Constatou-se, por evidências genéticas, que fêmeas dentro do grupo são mais aparentadas, enquanto que os machos são mais distantes (i.e. imigrantes) e caso fossem relacionados eles não reproduziriam (NIEVERGELT et al., 2000). Em alguns casos em que ocorrem conflitos entre fêmeas subordinadas e dominantes, pode surgir casos de infanticídios (BEZERRA; SOUTO; SCHIEL, 2007).

Com relação à sua biologia reprodutiva, a maioria das informações provém de cativeiro e demonstram que machos e fêmeas atingem sua maturidade sexual entre 12-15 meses (TARDIF et al., 2003) e podem produzir gêmeos duas vezes ao ano (GARBER et al., 2019), cujo filhotes aos poucos vão desenvolvendo habilidades motoras e ao mesmo tempo aumentam seu processo de independência (YAMAMOTO, 1993). O infante de *Callithrix jacchus* começa a exibir seu desenvolvimento motor logo quando nascem, conseguindo se segurar com os membros anteriores, por volta da segunda semana de vida desenvolve o tônus, até o vigésimo dia estará com a coordenação motora grosseira e preensão das patas traseiras desenvolvidas e por volta do trigésimo dia o indivíduo estará com a coordenação fina e tração muscular desenvolvidas (YAMAMOTO; ARRUDA; BUENO, 1986).

Um dos principais fatores que auxiliam na sobrevivência da prole é o cuidado cooperativo dos filhotes logo quando nascem (TERCEIRO; BURKART, 2019), sendo carregados principalmente pelo macho adulto (ZAHED et al., 2008) e também pelos

membros não-reprodutores (BALES et al., 2000; ROTHE et al., 1993). Yamamoto et al. (2008) observaram tanto em vida livre como em cativeiro, que os saguis-comum demonstram um certo viés sexual na hora de carregar os infantes, como por exemplo, os machos tendo preferência em carregar infantes fêmeas. Os recém-nascidos de calitriquídeos são carregados por vários membros quase que continuamente durante as três primeiras semanas de vida, ocorrendo interações durante seu transporte (YAMAMOTO, 1993).

A colaboração de outros integrantes do grupo inclui além de carregar, catar, compartilhar alimentos e proteger os filhotes contra potenciais predadores, poupar o gasto da fêmea dominante, assim como tais comportamentos promovem maiores chances de sobrevivência da prole e permite a aquisição de experiência no cuidado com os filhotes e também a tentativa de estabelecimento no grupo (YAMAMOTO, 1991). Rothe et al. (1993) verificaram, em seu estudo com *Callithrix jacchus* em cativeiro, que quanto maior o número de indivíduos em um grupo, maior o benefício do casal reprodutor em aliviar no carregamento dos filhotes. O cuidado parental em calitriquídeos, não é instintivo, é aprendido e estudos têm mostrado que se um calitriquídeo macho ou fêmea não teve experiência anterior com infantes de outra fêmea antes do nascimento de seus próprios filhotes, estes têm um maior índice de serem rejeitados e hostilizados (SAVAGE et al., 1995).

Os infantes de *Callithrix jacchus* podem ser influenciados pelo próprio ambiente que o cerca, afetando no cuidado parental e aloparental, como também no seu desenvolvimento (VENTURA; BUCHANAN-SMITH, 2003). Tardif et al. (1993) mencionam que recursos alimentares facilmente disponíveis e distribuídos a curtas distâncias, como exudados, podem provocar um desenvolvimento precoce dos infantes de *Callithrix jacchus*, tornando-os mais independentes no forrageio em relação a outros calitriquídeos.

Callithrix jacchus é o primata mais utilizado em pesquisas de laboratório entre os calitriquídeos (SMITH; HEATLEY, 2020). Em decorrência de sua fácil adaptação ao cativeiro e rápido amadurecimento, esta espécie tem se tornado um excelente modelo para pesquisas biomédicas (ABBOTT et al., 2003). Além disso, são amplamente estudados em outros estudos relacionado a aspectos de seu desenvolvimento, como por exemplo, habilidades motoras (WANG; FANG; GONG, 2014; WALKER; MACLEAN; HATSOPOULOS, 2016), ritmo circadiano (SENOO et al., 2011), vocal

(GHAZANFAR et al., 2018), visual (IZUMI; TSUCHIDA; YAMAGUCHI, 2011), neurobiológico (OKANO, 2021) dentre outros mecanismos biológicos.

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NUMBER OF ADULT FEMALES IN A GROUP AFFECTS INFANT MOTOR DEVELOPMENT OF A COOPERATIVE BREEDING PRIMATE (*CALLITHRIX JACCHUS*)

Alexandre Malta · Christini Caselli · Antonio Souto · María Fernanda De la Fuente · Nicola Schiel

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ORIGINAL ARTICLE

Number of adult females in a group affects infant motor development of a cooperative breeding primate (*Callithrix jacchus*)

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Abstract

Callitrichids are small Neotropical primates and, due to their cooperative breeding system, infants are of particular interest in research on social dynamics. Although a few studies have investigated the role of helpers in this type of system, there is still a lack of research in field studies seeking to determine whether there is a relationship between the number of helpers (adults) in a social group and the motor development of infants. With that in mind, four groups of wild marmosets (*Callithrix jacchus*) were observed and the motor behaviors of 1 to 4 month-old infants were recorded. To investigate the influence of the adult:infant ratio on motor diversity, used as an indicator of motor development, we ran a GLMM with a Gaussian distribution and found that: (i) in groups with fewer adults, 2-month-old infants show earlier motor diversity; (ii) motor diversity increases with age regardless of the ratio of adult males per infant; (iii) in groups with more adult females per infant, the motor diversity of 2-month-old infants is significantly lower compared to 3-month-old infants. Although adult callitrichid males play an important role in the care of their offspring, the presence of females appears to be a key factor in motor development at this early stage in the study groups. In a cooperative breeding system, the lack of helpers seems to drive the development of independence in infants, resulting in earlier development.

Keywords Primates · Helpers · Motor diversity · Common marmoset · *Callithrix jacchus*

Introduction

Living in social groups emerged as a key evolutionary response to survival in most primates (Mitani et al. 2012). While social-ecological models aim to identify the advantages and disadvantages of living in a social group with ecological and social factors as determinants (Terborgh and Janson 1996; De la Fuente et al. 2019), only a few investigate the possible effect of group size (Berman et al. 1997; Dunbar et al. 2018) or composition (Lehmann et al. 2007; Jablonski 2021; Markham and Gesquiere 2017) on infants' development (see also Hinde and Spencer-Booth 1968; Berman et al. 1997).

Callitrichids are small Neotropical primates that exhibit a precocial state in the level of development at birth, that is, they are more developed than newborn infants of altricial species (van Schaik and Isler 2012; see also Isler and van Schaik 2012; Schiel et al. 2010). Despite being considered "precocial", infants are dependent on adults for a prolonged period, during which motor and cognitive development occur (Schiel et al. 2010; Whiten and Waal 2018). In this respect, these species are of particular interest in research on social dynamics, especially when focused on the development and care of infants (Rapaport 2011; Huang et al. 2020; Saito et al. 2011). Social groups consist of up to ~ 15 individuals (Malukiewicz et al. 2021; Schiel and Souto 2017), which show intense cooperative care of offspring by reproducing and non-reproducing members (the latter are hereafter referred to as "helpers") (Ford et al. (2009); Rapaport 2011; Barbosa and Silva Mota 2013; Digby et al. 2011). The cooperative care of the offspring is probably due to the peculiar reproductive biology of these animals, which involves high costs such as (i) the birth of twins twice a year; (ii) a high maternal:neonatal weight ratio; and (iii) a postpartum estrus (Tardif et al. 2003, 2008). Thus, it is believed that

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helpers came to play a key role in the reproductive success of these small primates (Santos and Martins 2000; Rapaport 2011). In their study on captive *Callithrix jacchus*, Rothe et al. (1993) found that the greater the number of individuals in a group, the greater the benefit of the breeding pair in relieving the burden of caring for the infants. Furthermore, in a field study on *C. aurita*, Santos and Martins (2000) suggested that a greater number of helpers would be associated with slower development of the infants, presumably due to the easier access to food provided by the adults. Especially when it comes to the effect of the helpers' sex, males tend to carry the infants more often than females (Yamamoto and Box 1997), and a greater number of male helpers in a group seems to be associated with a higher survival rate of the infants (Koenig 1995; Garber 1997).

Although there have been studies attempting to understand the role of helpers (e.g., Tardif et al. 1995; Rapaport and Brown 2008), these usually focus on the animals that carry the infants (including the sex of the helper) and/or provide the most resources (Santos and Martins 2000; Yamamoto et al. 2008; Rapaport 2011). Moreover, a significant amount of data comes from studies on captive animals, which may represent a limiting factor considering the diverse environmental conditions that free-ranging animals are exposed to (e.g., Hinde and Spencer-Booth, 1968; Santos and Martins 2000; Stoinski et al. 2003). Thus, field studies investigating the relationship between group composition and the associated motor development in infants are still limited, and little is known about motor development in young primates (see Young and Shapiro 2018).

Common marmosets (*Callithrix jacchus*) stand out as a promising model for studies on the effects of social interactions (De la Fuente et al. 2019, 2021), as they are characterized by a cooperative breeding system (Schiel and Souto 2017), associated with a sensitive period of infants' motor and cognitive development (Schiel and Huber 2006; Schiel et al. 2010; Wang et al. 2014; Young and Shapiro 2018). Factoring in greater ease in obtaining care from adults, we expect that a larger number of adults in the group would lead to delayed motor development in infants (prediction i). Moreover, given that males carry the infants more often, we expect that in groups with more males the infants would show a delayed motor development (prediction ii); and that, on the other hand, the number of females in a group would not affect infants' motor development (prediction iii).

Methods

Study area

Sampling was carried out in a residential condominium within the Aldeia-Beberibe Environmental Protection Area (31.634 ha; CPRH 2022) featuring fragments of primary and secondary Atlantic Forest, with areas inhabited by humans and areas entirely forested (for a further description of the area, see Souto et al. 2007). The area is in the township of Camaragibe (7°56′97″S, 35°1′23″W), in the state of Pernambuco, northeast Brazil. Several studies have been conducted in the area since 2001 (e.g., Schiel and Huber, 2006; Souto et al. 2007; Schiel et al. 2010; Gunhold et al. 2014).

Subjects

Four groups of wild marmosets totaling 29 individuals were observed (Table 1). The members of each group were identified by sex, size, and their natural markings, such as the size and color of ear tufts, facial scars, hair color, and physical impairments (Schiel et al. 2006). All animals were habituated to the presence of the researchers (Schiel and Huber 2006; Bezerra et al. 2007; Gunhold et al. 2014). Based on the age categories established by Ingram (1977), we classified the animals into adults/sub-adults (≥ 11 months), juveniles (5–10 months), and infants (1–4 months). Table 1 shows the composition of the four observed groups and the individual:infant ratio of these groups (for more details see the data analysis section). During the observations, the composition of the groups remained stable, except in group C, where a new male joined the group immediately after the disappearance of the dominant male. This research study was conducted in compliance with the guidelines for the ethical treatment of animals in behavioral research and teaching (Animal Behaviour 2003; v.65; p 249–255), as well as with the ethical principles for the treatment of non-human primates, established by the American Society of Primatologists.

Table 1 Group composition and ration for each studied group

Group composition					Adult:infant ratio			
Group	Adult	Adult ♂	Adult ♀	Juvenile	Infant	Adult:infant	Male:infant	Female:infant
A	6	3	3	2	2	3 (more)	1.5 (more)	1.5 (more)
B	4	1	3	0	1	4 (more)	1 (less)	3 (more)
C	4	2	2	2	2	2 (less)	1 (less)	1 (less)
D	4	3	1	0	2	2 (less)	1.5 (more)	0.5 (less)

Procedures

Sampling occurred from October/2001 to April/2002, between 6:00 a.m. and 5:00 p.m., 5 days a week. The observations were carried out using the focal animal method (Altmann 1974; Lehner 1996), with continuous 10-min sessions, for a total of 600 h of observation. All infants were observed for the full 4 months. When an animal was lost from view for a period ≥ 1 min, the session was discarded. All observations were recorded using micro-cassette recorders (Sony M-529 V; Aiwa NFR TP-M330) for later transcription and analysis in Excel spreadsheets.

Importantly, we are using motor diversity as an indicator of motor development, as they are intertwined (Adolph and Robinson 2015; Yamamoto 1993). Thus, we were attentive to the following infants' behavioral events: prey capture, prey capture attempt, prey stealing, crawling, minor locomotion, major locomotion, traveling, gummivory, weak pounce (with or without prey capture), strong pounce (with or without prey capture), leaf/branch/fruit manipulation with hand/mouth (for the definition of these behaviors see: Schiel and Huber 2006; Schiel et al. 2010; Ngo et al. 2022).

Statistical analysis

First, to measure the motor activities of infants based on the observed behaviors, we calculated a motor behavior index (MDI: Motor Diversity Index), which reflects the motor ability of each infant during each month of age (1 to 4 months). To this end, we used the Shannon Index, combining the different types of behavior and their frequency:

$H = -\sum_{i=1}^{s} \frac{ni}{N} \ln \frac{ni}{N}$

ni corresponds to the number of each behavior, *N* is the total number of sampled behaviors, and *ni*/*N* is the relative abundance of each behavior. H reaches its maximum when all behaviors occur at equal frequency. The higher the final value, the greater the diversity.

Before testing prediction (i), we examined whether the MDI value was related to the number of sessions sampled for each infant, given that a greater number of sessions could mean a greater chance of observation/sampling a new motor behavior. To accomplish this, we ran a generalized linear mixed model (GLMM) with a Gaussian distribution (normal data), where the MDI value was the response variable, the number of sessions for each age group of each infant was the predictor variable, and the group identity was the random variable (controls the group effect). The results showed that MDI is not affected by the number of sessions (GLMM: $F_{1,19} = 0.30$, $p = 0.59$). Therefore, the MDI was used as the response variable to test prediction (i).

Next, we compared motor diversity across infants' age groups (1 to 4 months) to examine among which age groups the MDI differs, and to understand which age groups could be included in our analysis to test how group composition affects motor development in infants. This was done by building a GLMM with Gaussian distribution, where the response variable was the MDI, the predictor variable was age (categorical: 1 to 4 months) and the control variable was the group identity. For this model, we allowed heterogeneous variance among different age groups (following Zuur et al. 2009). We found that motor diversity (MDI) varies with age (GLMM: $F_{1,17} = 72{,}81$, $p < 0.0001$). Tukey's post hoc test (pairwise comparison) showed that the MDI differs between month 1 and months 2, 3, and 4 ($p < 0.0001$, Fig. 1), as well as between months 2 and 3 of age ($p = 0.021$, Fig. 1). Since 1-month-old infants are carried most of the time and do not yet have a good motor development (Yamamoto 1993), this age group was removed from the analysis. The 4-month age group was also removed because motor diversity at this age seems to be already developed (Schiel et al. 2010). Therefore, to test our hypothesis, we used 2- and 3-month-old age groups, where motor diversity varies significantly.

Since the number of infants and adults varies between groups, we calculated the adult:infant ratio in 2- and 3-month-old infants to find the ratio of adults per infant in each group. We then grouped these values into the categories "more" and "less" adults as our corresponding predictor variable for group composition. The same procedure was used to calculate the adult male:infant ratio and the adult females:infant ratio (see Table 1). This ratio was calculated by accounting for all adult individuals in each group, including the reproducers. We assumed that the number of breeding adults among groups remains constant (with each group having one breeding female and one breeding male), so the variation in group composition differs according to the number of non-breeding individuals (helpers). Since we have no

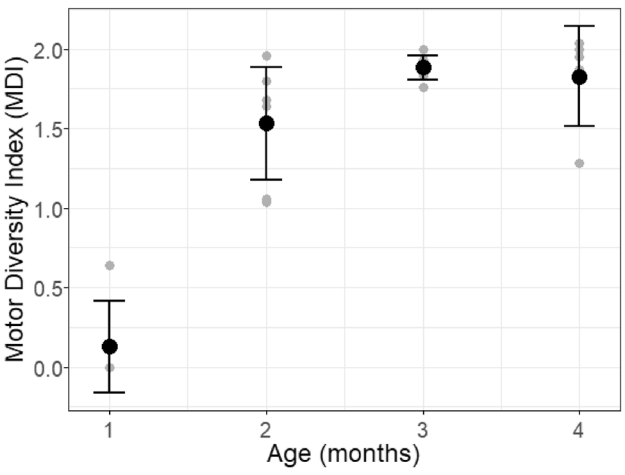

Fig. 1 Motor diversity of common marmoset infants by age (months). Tukey's post hoc test (pairwise comparisons): different letters represent significant differences ($p < 0.05$)

genetic information about the identity of the breeding male, we chose to include all adults to avoid possible identification biases. Juveniles were not included in the analyses since they play a minimal role in infant care (Yamamoto and Box 1997).

Finally, to investigate the effect of adult:infant ratio on motor diversity in 2- and 3-month-old infants, we ran a GLMM with Gaussian distribution where the response variable was the MDI, the predictor variables were infants' age (category: 2 and 3 months) and adult:infant ratio (category: "more" and "less" adults per infant), and the random variable was once more the group identity. To further investigate whether the adult male and adult female ratio have a different effect on the motor diversity of these infants, we built two GLMMs with Gaussian distribution by replacing only the adult:infant ratio variable of the first model with the adult male:infant ratio variable and the adult female:infant ratio variable, respectively.

The statistical software R, version 4.1.1 (R Core Team 2021), was used for all the analyses. All models (GLMMs) were fitted using the "lme" function of the "nlme" statistical package (Pinheiro et al. 2019). We compared the models (null vs. full models) by sequential analysis of the variance using the Anova function from the R Stats package. To conduct pairwise comparisons (Tukey's test), we used the lsmeans package (Lenth 2016). Before running the comparisons, we examined the models against the assumptions of normality and homogeneity. When the assumption of homogeneity of variance was not met, heterogeneity of variance was incorporated into the model, since it may provide relevant ecological information. The significance level set for all analyses was $p \leq 0.05$.

Results

The results show that the interaction between age and the composition of adults in the group (adult:infant ratio) affects infants' motor diversity (GLMM: $F_{1,8} = 5.49$, $p = 0.047$). More specifically, considering that motor skill is already high by infants with 2 months (see Fig. 1), in groups with fewer adults per infant, motor diversity is similar across the 2- and 3-month age groups, while in groups with more adults per infant, motor diversity of 2-month-old infants is significantly lower than 3-month-old infants (Fig. 2a). This supports our prediction (i) because in groups with fewer adults 2-month-old infants develop earlier than infants in groups with more adults.

When the effect of the adult male:infant ratio on motor diversity was investigated separately on 2- and 3-month-old infants, motor diversity was found to be affected by age only (GLMM: $F_{1,8} = 11.18$, $p = 0.01$), and not by the male:infant ratio or the interaction between the two variables (GLMM: $F_{1,8} = 0.42$, $p = 0.53$). That is to say that infants' motor diversity increases with age regardless of the ratio of adult males per infant in the group (Fig. 2). When investigating the influence of adult female:infant ratio, we found that it affected infant motor diversity in the same way as the overall adult composition (GLMM: $F_{1,8} = 5.49$, $p = 0.047$). In groups with fewer adult females per infant, motor diversity is similar across the 2- and 3-month-old age groups, while in groups with more adult females per infant, motor diversity of 2-month-old infants is significantly lower than 3-month-old infants (Fig. 2).

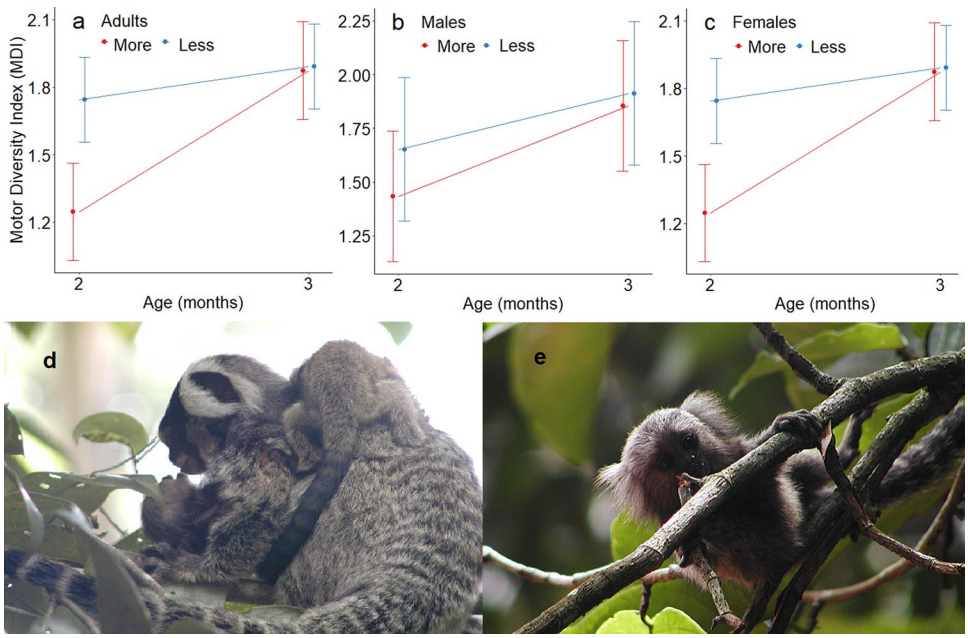

Fig. 2 Motor diversity index of 2- and 3-month-old infants: **a** with more and less adults per infant; **b** with more and less adult males per infant; **c** with more and less adult females per infant; **d** 3-week-old infants on their mother's back; **e** 2-month-old infants exploring (photos by Antonio Souto)

Discussion

This study investigated whether group composition affects the motor development (as indicated by motor diversity; Adolph and Robinson 2015) in infants of wild common marmosets, which are primates characterized by a cooperative breeding system. We found that having more adults in the social group delays the motor development of infants, which supports our first prediction. Santos and Martins (2000) suggested that the presence of more helpers in a group could lead to a delay in motor skills in infants, which in turn leads to a delay in the ability to get solid food independently. The same seems to be true in our study. Thus, the lack of helpers would accelerate independence in infants, resulting in earlier development.

On the other hand, in contrast to our prediction, the advanced motor development of infants from larger groups appears to be affected by the ratio of adult females per infant, rather than by the ratio of adult males per infant. Thus, it seems like the presence of more females in a group slows down the motor development of 2-month-old infants. Although adult callitrichid males play an important role in caring (e.g., carrying and sharing food) for their offspring (Santos and Martins 2000; Burkart 2015; Yamamoto 2005; Ziegler et al. 2017), the presence of females seems to have been a key factor in motor development at this early stage in the study groups. While Kostan and Snowdon (2002) observed the adult males of cotton-top tamarins (*Saguinus oedipus*) to be the attachment figures for infants (especially under stress situations), it should be mentioned that Tardif et al. (1993) found that, although males were the primary carriers, mothers were always preferred as a "contact partner". Such a preference could be associated with the fact that infants prefer females over males as role models (Schiel and Huber 2006). These two complementary aspects seem to be crucial to explain the longer development time in groups with more female individuals. Our results are comparable to those obtained with rhesus monkeys, in which more prolonged contact with the mother would delay the development of independence in infants when it comes to locomotion on the ground (Maestripieri et al. 2009). Although our study is focused on a species that exhibits cooperative care by group members, the comparison is still useful, since in our case there seems to be a stronger bond with all the females of the group rather than with a specific female, as documented in rhesus monkeys (see also Vochteloo et al. 1993; Maestripieri 2018).

It might be tempting to evaluate the earlier motor fitness of marmoset infants in larger groups as positive and assume it to be true for smaller groups as well. However, caution is needed when evaluating earlier independence as positive or negative without considering some important aspects. For example, it is well known that dependence on caregivers at a stage of biological and/or psychosocial immaturity means protection from starvation and predators (e.g., Fragaszy and Bard 1997). Thus, large groups of marmosets would provide greater protection, in turn, allowing the infant to explore the environment more safely than when in a small group. This possibility to explore more would presumably be a facilitator for the motor development of infants, as observed in our study. It is also worth noting that in humans, except in extreme cases such as abandonment, situations characterized by both greater and lesser dependence have positive aspects for the motor development of children. Thus, the "attachment theory" has shown the positive psychological implications of close and harmonious social relationships, which can produce an increase in the child's self-confidence, with benefits when it comes to the exploration of the environment (e.g., Holmes 2014; van Londen et al. 2007). However, as previously mentioned, motor skills such as teeth-brushing or bathing alone were facilitated in groups whose mothers needed to go to work in the fields (Wulan and Kurniawati 2020). Therefore, as long as there is no premature independence or excessive care (something hard to imagine in non-human primates in the wild), both strategies would have survival benefits, depending on ecological, biological, and/or psychosocial aspects.

Overall, our results showed that more helpers lead to delayed development, and females seem to have a greater effect on this process. While most studies address the identity and/or the role of the helper, little is known about how these variables impact the motor development of infants. In addition, environmental and mental factors, such as personality (see Šlipogor et al. 2021) may affect infant care. Thus, while data is still scarce and more studies are needed to better understand motor development in primate infants, we hope our study will encourage further investigations on this fascinating subject.

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Author contributions Conception: AS, CC, MFDF, NS; design of the study: CC, MFDF, NS; sampling: NS; data analysis: CC and MFDF; writing of the article: all authors. All authors have read and approved the final version of the article.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest to declare.

Ethical approval The present research study was conducted in compliance with the guidelines for the ethical treatment of animals in behavioral research and teaching (Animal Behaviour, 2003; v.65; p 249–255), as well as with the ethical principles for the treatment of non-human primates, established by the American Society of Primatologists.

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