The ontogeny of play in a highly cooperative monkey, the common marmoset

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Abstract

Play is widespread in mammals. It is mostly observed in juveniles and has been subdivided in three categories, social, locomotor/rotational, and object play. Although there is no strict consensus on its ultimate function, the dominant idea is that through play juveniles acquire social, technical and cognitive skills for their adult life. In certain species, however, adults remain playful especially with immatures. This pattern can be observed in particular when same-age play partners for immatures are lacking and if adults also invest in caretaking. We studied the ontogeny of play in cooperatively breeding common marmoset twins from the age of two to six months. Social play increased with age and was by far the most prevalent category. Play partners varied with age. Before 19 weeks old, immatures played 54% of the time on average with either one of their parents (in a dyad) and 29% on average after 19 weeks old. Thus, despite the constant presence of a twin, adult-immature play remained considerable, with equal contributions by mothers and fathers and no trade-offs with other care-taking behaviours for either of the parents. However, parents avoided playing simultaneously, presumably to avoid periods with no one vigilant. Together these results show that parents are important play partners for marmoset infants, fathers and mothers alike.

Keywords: common marmoset; play behaviour; play ontogeny; social play; parental investment

Introduction

Play behaviour is widespread among mammals, and some orders are especially known for their playfulness, such as rodents, carnivores or primates (Burghardt, 2005; 2014). In all those species, play is most prominent in juveniles, even though it can sometimes persist into adulthood as observed in dogs, bonobos, or humans (Boere et al., 2020; Bradshaw, 2015; Burghardt, 2005; Hare et al., 2007; Pellegrini, 2009).

In the non-human animal (henceforth animal) literature, play is generally split into object play, locomotor-rotational (L/R) play and social play (Burghardt, 2005). Object play involves object manipulation without any apparent purpose, but is not always easily distinguished from object exploration and tool use (Pellegrini & Smith, 2005). L/R play is usually defined as any locomotor

movement e.g., jumping, running, rolling, again with the additional specification of having no apparent purpose. Object and L/R play can either be solitary or integrated into social play. Social play involves two or more players that are usually conspecifics (Graham & Burghardt, 2010). The latter is the most frequently studied of the three play types and is also the most prominent in mammals and birds (Burghardt, 2005). Within social play, play fighting also known as Rough-and-Tumble play is most recognizable. Rough-and-Tumble play mimics real fights and aggressive behaviours but the players very rarely come out of a play fight wounded (in humans: Smith, 1997), conversely to real aggressive contexts (Palagi et al., 2016; Pellis & Pellis, 2017). Play does not occur uniformly throughout animals' life but follows an inverted-U-shape distribution with an early appearance during infancy, a peak at juvenile age and a slow decrease after this period (Panksepp, 1981; Pellegrini & Bjorklund, 2004). The fact that play behaviour almost disappears at a certain stage of an individual's life indicates either that benefits from playing can only be gained during the immature period (Pellis et al., 2010) or that the costs are too high at a certain point (Pellis & Iwaniuk, 2000). Three main costs associated with play behaviour have been identified in the literature: increased predation risks (Harcourt, 1991; Hausfater, 1976), energetic expenditure (Kunz et al., 2024; Pellegrini et al., 1998) and risks of accidental and social injuries (De Oliveira et al., 2003). Unfortunately, only a few studies have directly investigated these risks and quantified the costs during play e.g., predated animals during play, energy loss in kilocalories, wounds after a play fight (Pellegrini et al., 1998).

Despite the associated costs, immatures are highly motivated to play. Human children who have been stripped from their opportunities to play for some period, show increased play durations of play when opportunities can be resumed (Pellegrini et al., 1995; Pellegrini & Davis, 1993; Smith & Hagan, 1980). The same has been shown in multiple species, such as rats (Holloway & Suter, 2004), calves (Jensen & Kyhn, 2000 but see Bertelsen & Jensen, 2019) or pigs (Wood-Gush & Vestergaard, 1991). Moreover play deprivation leads to less flexibility in animals' social behaviour and impaired social reactions (e.g. Syrian hamsters, Mesocricetus auratus: Cooper et al., 2023; Wistar rats, Rattus norvegicus domestica: Hol et al., 1999). This combination of high urgency to play and costs of playing in immatures suggests that there is an important biological function to this behaviour (Bond & Diamond, 2003).

There is no strict consensus on the ultimate function of play in the literature. One dominant view has been that play is a way for juveniles to acquire skills for their adult life (Bateson, 2005; Pellegrini, 2009). Those deferred benefits encompassed hypotheses about a motor training function (Berghänel et al., 2015 but see Byers & Walker, 1995; Pellis et al., 2023), an enhancement of social skills (Ahloy Dallaire & Mason, 2017; Blumstein et al., 2013; Pellis et al., 2010 but see Sharpe, 2005), a cognitive training function (Biben et al., 1989) as well as 'training for the unexpected' (Spinka et al., 2001). Shorter term benefits of social play have been ascribed to xenophobia reduction (Antonacci et al., 2010), social assessment (Pellis & Iwaniuk, 2000) and stress relief (Kyle et al., 2019). Pellegrini et al. (2007) have also argued that immediate benefits could be that juveniles learn to know their environment and can rehearse behavioural responses while avoiding high social risks. Besides these hypotheses that focus on (more or less) delayed benefits, research on laboratory rats (as well as mice and hamsters) has provided a model to study functions of play fighting and its influence on brain development. There is convergent evidence that juvenile play has an effect on pruning of neurons in the medial prefrontal cortex as well as the physiological characteristics of these cells (Burleson et al., 2016; Byers & Walker, 1995; Pellis et al., 2023). Moreover, in primates the relative size of certain areas of the brain i.e., neocortex, cerebellum, amygdala, hypothalamus, striatum have been shown to

correlate well with social play frequency (Graham & Burghardt, 2010; Lewis & Barton, 2004, 2006; Montgomery, 2014), hinting at play having a organisational effect in the developing brain.

Play is clearly the realm of juveniles, but in certain species adults continue to play at a high rate. This is puzzling because the important benefits of play are mainly associated with the juvenile period and the same costs described for the immatures apply to the adults as well and should prevent them from playing. While playing, adults do so at the expense of their caloric and time expenditures, as well as their own safety and the one of their offspring by lowering their vigilance whereas they should be increasing it i.e., while immatures are playing they are more vulnerable to predators, adults would thus be expected to protect the immatures with increased vigilance (Biben et al., 1989; De Oliveira et al., 2003; Harcourt, 1991; Hausfater, 1976).

Certain factors seem to favour play behaviour from adults with immatures. First, the level of social tolerance in a group (Palagi, 2023; Palagi, Cordoni, et al., 2016) and the fluidity of the relationships (Pellis & Iwaniuk, 2000a) could facilitate social adult play. Further, parents investing time and energy in rearing their offspring, often the primary caregiver(s), will often be seen playing with them e.g., chimpanzees Pan troglodytes (Pellegrini & Smith, 2005), orangutans Pongo spp. (Fröhlich et al., 2020) or wolves (Essler et al., 2016) although this is not always the case. For example, in squirrel monkeys Saimiri boliviensis (Biben et al., 1989) and rhesus macaques Macaca mulatta (Kulik et al., 2015; Tartabini, 1991), mother-infant play is rarely or never observed. A factor that could explain those differences between species is the presence or absence of other immatures. It has been suggested that immatures prefer playing with their peers, and will play with adults if there are no other options (Kunz et al., 2024; Pellis & Iwaniuk, 2000; Poirier, 1970). Ultimately it has been suggested that, by playing with infants, adults facilitate the immatures' acquisition of species-specific signals and skills employed in various social interactions (Enomoto, 1990; Mackey et al., 2014; Paquette & StGeorge, 2023; Sutton-Smith, 1993). Adults would thus invest time to pass down, voluntarily or not, some social skills (Paquette et al., 2003) and may ultimately contribute to increase the fitness of the immatures (Amodia-Bidakowska et al., 2020).

The goal of this study was to investigate the ontogeny of play, with a special focus on parent – infant play in common marmosets. We longitudinally documented play, in three groups with infants between two and six months old. All groups were comprised of two breeders and two infants without helpers. Marmosets are cooperative breeders, where non-mother individuals provide care for the juveniles and are part of the broader family of callitrichids. Callitrichid monkeys are known for their high level of social tolerance and general prosociality, characteristics that are directly linked to their cooperative breeding system (Burkart & van Schaik, 2020; Hrdy & Burkart, 2022). Groups are usually constituted of two breeders and several sexually mature helpers. All contribute to rearing the infants. Adult breeders and helpers appear to show a genuine concern about the immatures' well-being (Brügger et al., 2018, 2023) and proactively share food and information (Sehner et al., 2023). Males are important caretakers for the immatures, in contrast to most of the other primate species (Burkart et al., 2007). Additionally, females generally give birth to twins (Haig, 1999).

We first investigated the ontogeny of object, L/R and social play, predicting that all three categories should increase in frequency as the infants matured. Following the studies on marmoset play behaviour from Stevenson & Poole (1982) and Voland (1977), we expected social play to be the most prominent category of play. We expected to see very little object play since the species-specific

distribution of the different play categories seems to be related to differences in the behavioural repertoire of those species in adulthood i.e., while immature chimpanzees (Pan troglodytes), where adults are known to be skilled tool users engage in object play, their sister taxa bonobos (Pan paniscus), who are not frequently using tools, show comparatively less object play (Koops et al. 2015, Pellis&Pellis 2017, Pellegrini&Smith 1998) and marmosets are not known to use tools at all.

We then explored infants' partner preference, predicting that they would prefer to play with their parents initially and this would decrease over time to be replaced by twin play. Parent-infant play is age-sensitive and tends to be more prominent in young infants than juveniles (Amodia-Bidakowska et al., 2020; Kunz et al., 2024; Mackey et al., 2014; Paquette & StGeorge, 2023). In early studies on common marmosets (Voland, 1977) it has been found that immatures prefer to play with their twin rather than adults (Voland, 1977), but Stevenson & Poole (1982) suggested that partner preference depends on the age of the immatures and adults could be important play partners at an early stage of the infants' development. Knowing that marmosets are highly tolerant and adults contribute actively to infant care we thus expected adults to engage in play at high rates, especially at very early developmental stages.

Zooming in on parent-infant play, we looked at each parent separately, to see if mothers and fathers would play to a similar extent with the infants. Sex differences in play styles and frequencies are generally associated with the social structure of a species and sexual dimorphism. In several monogamous species who do not show sexual dimorphism such as wolves Canis lupus (Cordoni, 2009), cotton-top tamarins Saguinus Oedipus (Cleveland & Snowdon, 1984) or grasshopper mice Onychomys leucogaster (Pellis et al., 2000), sex has reportedly no influence on play style. Stevenson & Poole (1982) however found that adult males played more than did adult females, and they showed that it was linked to the reproductive state of the females.

Since play can take a toll on the immatures' fitness by reducing their focus on antipredator vigilance,we expected parents to take into account this risk and act accordingly by taking turns when playing, especially in small groups. First, callitrichids are known to coordinate vigilance. For instance, marmoset dyads take turns in being vigilant (Brügger et al., 2023; Phaniraj et al., 2023), and tamarins increase their vigilance when infants are at play (De Oliveira et al., 2003). Second, if parents are important play partners, it might be that they often have to compromise their own vigilance level, and thus the only solution to stay alert at the group-level is for one individual to stay vigilant while the other cannot. We thus examined whether and how much the father and the mother played simultaneously i.e, we searched for all overlaps of time when both parents were playing to see if they actively avoided playing together with the infants or not.

In callitrichids, female breeders experience high reproductive costs due to twinning and post-partum oestrus (Beehner & Lu, 2013; Leutenegger, 1973). It is likely that they have to compromise by playing less, since it is an energy-consuming behaviour (Guerreiro Martins et al., 2019). In contrast, male breeders tend to be more flexible in the participation of energy-consuming activities depending on the presence or absence of helpers, as observed for example in carrying behaviour (Snowdon & Ziegler, 2007; Yamamoto et al., 1996). When no helpers are present, fathers tend to carry the infants more. In their study, Stevenson & Poole (1982) observed play in extended family groups comprising helpers but since no helpers were present in our study groups, we expected that the difference

between fathers and mothers' playful investment would be even higher, with male breeders being much more playful.

To understand how father-infant and mother-infant play relates to typical measures of investments level into infant rearing, we investigated its potential correlation with individual contributions to food sharing and infant carrying. We expected both carrying and food sharing rate to positively correlate with the amount of play from the fathers, but we expected to see a trade-off in mothers, with females investing more in one of those activities to invest less in the others

Methods

Subjects and housing

We collected observational data on three family groups (N = 12) of captive common marmosets. The groups were observed when immatures were between 2 and 6 months old (see additional information for group composition and data collection details in Table S1). All groups had immature (between age 0–2 months) or juvenile (between 3–6 months) twins and none had helpers (Abbott et al., 2003). The groups were thus constituted of two breeders and two immatures.

All individuals were captive-born, parents-reared and housed in family groups. Their heated indoor enclosures were equipped with various climbing materials (branches, ropes, tubes, and platforms), a sleeping box, an infrared lamp, and floors covered by bark mulch. The animals had regular access to outdoor enclosures when weather conditions were adequate. Feeding of all animals occurred once in the morning at 08h00 with a vitamin-enriched mash and at around 11h30 with a variety of vegetables. During the afternoon, the marmosets received diverse additional protein sources such as insects or eggs. Before, during and after the observations, water was always available through water dispensers.

Data collection

Video-recordings

All sessions were collected with either two or three GoPro cameras (Hero7 white with a resolution 1920*1440 pixels and Hero9 black with a Wide Quad HD resolution). The cameras were placed to ensure almost full visual coverage of the enclosure by placing one camera at the front, one at the back of the enclosure, and additionally one on the ceiling, for a duration of 30 minutes. The trap door leading to the outdoor enclosures was always closed during the recordings. No experimenter was present during the video- recordings.

To provide an attractive play platform, a hammock (large towel) was placed in the enclosure and clipped to the mesh ceiling during the sessions. Old jeans or towels are already part of the standard equipment of home enclosures and marmosets spend a lot of time playing in/on them. We thus replaced them by a new hammock (large towel) in a way that allowed optimal visibility for the cameras.

We collected data on the three groups regularly between 2 and 6 months of the age of the immatures, keeping the balance between the different periods of the day to avoid any unwanted bias

(Norscia & Palagi, 2011): before feeding (BF) 09h–11h and after feeding (AF) 13h–14h. Two sessions (one BF and one AF) were recorded almost every other week for each group during five months. Overall, a total of 66 sessions were collected corresponding to 1980 minutes of video material. All the individuals from the groups were visible during the recordings, which means that 660 minutes of videos were collected for each individual of each group.

Food sharing and carrying data

For each breeder, immature carrying was recorded daily between 8 am and 5 pm in hourly group scans for 120 days after birth.

To evaluate how much food each parent would share with the immatures depending on their age, we followed the food sharing protocol described in Guerreiro Martins et al. (2019), twice a week during the whole data collection period (see Table S1). The high value food to be shared, a defrosted cricket, was but distributed in a standardised manner, one item at a time and one adult at a time. During each food sharing session three crickets, i.e., three trials, of approximately the same size were sequentially provided to each adult. For each trial, we observed if the cricket was shared or not and: if it was shared proactively (food calls from the donor before any begging from the immatures), reactively (begging from the receiver happened before the donor food called if she or he food called at all), resisted (food was transferred but adults showed resistance by chatter calling and/or running away from the begging individual), and who the recipient was. If the cricket was not shared, we also recorded if others had begged (refusal, i.e. no sharing despite begging). . During the first months we could not distinguish between the twins as they had no distinguishable marks; they were thus counted as "immatures". AMG and RKB collected the food sharing data for the Washington and Jambi groups. Sandro Sehner collected data for the Guapa group. We ensured inter-observer reliability by having 14% of all food sharing trials collected by two raters simultaneously. A Cohen's kappa of 0,64 was reached.

Ethical Note

All experiments were carried out in accordance with the Swiss legislation and licensed by the Kantonales Veterinäramt Zürich (licence number: ZH232/19). All of the experimental procedures were fully non-invasive (degree of severity: 0) as most of them were only behavioural observations and the rest (food-sharing experiments) were about giving the individual highly valued food items (crickets). No experiments were conducted outside the home enclosure and no animal was food or water deprived during any point of this study.

Data coding and preparation

We conducted frame-by-frame analyses (25fps or 29.97fps) using the software INTERACT (Mangold GmbH, version 18.7.7.17). We coded the videos using focal sampling (Altmann, 1974), thus for each video analysed, we collected the relevant data from all the individuals of that group.

Coding

Play definition. We identified play behaviour following Burghardts' (2005) five criteria:

(1) The behaviour is not fully functional in how it was expressed, and thus did not contribute to immediate survival
(2) The behaviour is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic
(3) Compared to functional behaviours it is either incomplete, exaggerated, awkward, precocious, or modified
(4) The behaviour is repeated throughout the development of the individuals, but not in a rigid stereotypical way
(5) The behaviour is observed when the animals are relaxed and not under stress or competition

Further, we made sure to exclude real fight situations from social play. During real fights both the aggressor and the victim produce chatter call vocalisations, and the attacks are only unilateral with a clear dominant (Bezerra & Souto, 2008; Stevenson & Poole, 1976). The bites are also usually not inhibited which means that wounds can be visible afterwards. Moreover, intra-group aggression rates in marmosets are known to be rare (Finkenwirth & Burkart, 2018).

We defined play operationally as any social or solitary component present in our ethogram occurring while focal sampling the individuals. Social play included two or more individuals and was either performed unilaterally i.e., a play element was directed towards a playmate or bilaterally i.e., a play element was reciprocated and both playmates were attacking. Solitary play included object manipulation and locomotor/postures play.

The ethogram (Figure 1) was made using the marmoset play ethograms of Stevenson & Poole (1976, 1982) and Voland (1977). Further additions were made with the help of other play behaviours described in Petrů et al. (2009) and (Cordoni & Palagi, 2011). In addition to the illustrated ethogram, supplementary video material of all coded play behaviours is provided (Section S3).

A coding protocol (see the protocol in Table S2) with refined definitions was established to facilitate recognition of each play element. For components with a duration, this included when the exact start and end had to be coded (see Figure 1 for details about which play elements were coded as durations or events). Importantly, the following rules were implemented during video-coding:

1. For the social play elements, the focal individual was always chosen in function of the initiation: she was chosen if she was the first one to make physical contact i.e., during wrestle or pulling, or the one doing the action i.e., chasing another one or doing a supine.
2. No individual could be twice a focal individual at the same time. This choice was made to not code several behaviours at the same time coming from the same individual. We decided to prioritise social elements before solitary ones e.g., two individuals wrestling in an acrobatic position because they were hanging from the hammock was only coded as wrestling and not as doing an acrobatic posture. We then prioritised elements with durations before events e.g., if an individual chasing another one and managed to touch the chasee while running, the touch was not coded.

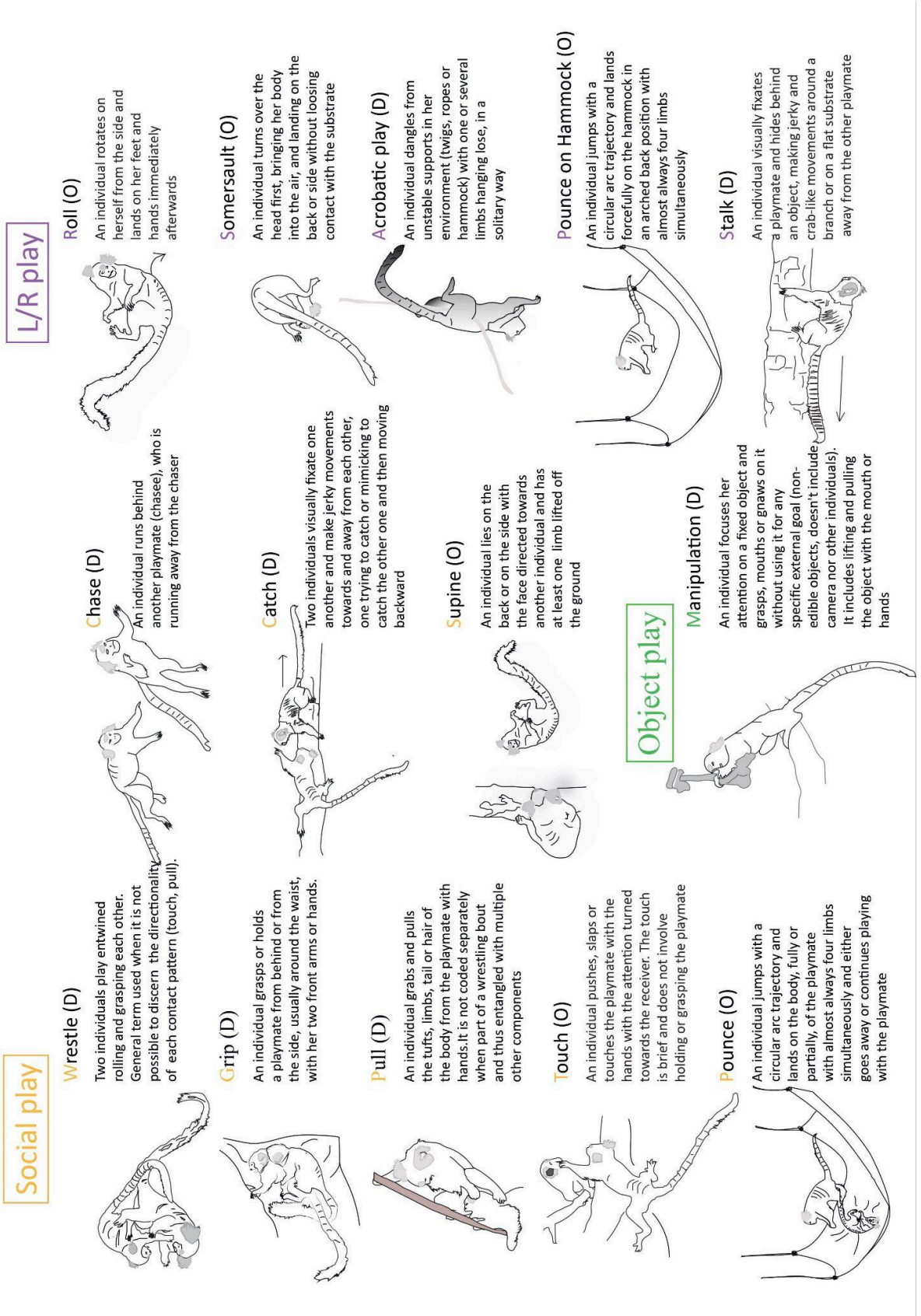

Figure 1. Illustrated ethogram with all the play elements coded in the present study. The playful elements were classified into three bigger categories: Social play, L/R play and object manipulation. (D): play element coded with a duration, (O): play element coded as an occurrence.

If one individual was totally hidden behind an object in the enclosure and thus not visible, she was coded as out of sight (oos). If two individuals were playfully interacting but the behaviour was either not described in the ethogram or not fully visible from the cameras, it was coded as 'unknown' (UK) , thus acknowledging that there was play but without inferring what it was. UK play elements could either have duration or be coded as states and could be solitary or social. For all analyses regarding play amount between dyads or triads, the UK play elements were included. We proceeded the same for solitary play elements that were not described in the ethogram.

Because at the beginning of the video-recordings the twins of each group were not recognisable, they were coded indiscriminately as immatures. In summary, the following variables were coded: players identity, frequency or duration of the play items, including UK elements, directionality of the social play elements (who is performing the action towards whom), for the element "pull" what was the target (tail, hair of the body, tufts or limbs) and for the element "acrobatic play" where it was happening (towel, rope, twig).

In total across the three groups, we coded 1060 minutes randomly chosen from among the sessions. This represents approximately 20 minutes of video footage in one or two different sessions for each month of the immatures' life between 2 and 6 months and for all individuals of each group. In summary, for each video analysed, we coded the identity of the players, the exact sequence of each play interaction (Figure 1) and the exact duration (seconds) or occurrence of each play element.

We assessed inter-observer reliability for each play element with a second rater (Melanie Meyer) who coded 9,4% of the videos, by looking at intraclass correlation coefficients (ICC 3) for each play element that we coded, either by using the duration or the occurrence of those elements. Roll and somersault were excluded from the IOR because only one element of each was present in the selected video bouts for the IOR. Overall, those two components were very rare and thus excluded from all analyses (Table 1).

Table 1. Inter-observer reliability for all the play elements coded.

Play element	ICC	duration(D)/ occurrence(O)
chase	0.97	D
wrestle	0.99	D
pull	0.93	D
stalk	0.93	D
catch	0.89	D
grip	0.93	D
supine	0.86	O
touch	0.81	O
pounce	0.96	O

pounce on hammock	0.99	O
manipulation	0.98	D
acrobatic play	0.38	D
somersault	excluded	O
roll	excluded	O

Data preparation

Part 1: Play trajectories

We calculated the frequency at which immatures performed social, locomotor and object play elements as the number of times that the immatures performed a social, locomotor or object play element out of the total time observed in a specific session. All play instances were taken into consideration, no matter the play composition (dyads or triads). We adjusted for the time the immatures could have been focal or receiver of a play element but one of the potential players was out of sight by subtracting from the total time observed the time when at least one individual was out of sight.

Part 2: Partner preference

Since coding play with separate elements leads to non-continuous play interactions, a suitable period needed to be defined which would summarise elements that can be considered linked together into a play bout. In other words, we needed to decide what could be considered a play bout between two individuals and how long an interval of time had to be for two play bouts to be considered separate.

Different interval lengths are found in the literature (Hawley, 2016: 1 minute for gorillas, Heesen et al., 2021: 3 seconds for bonobos, Stevenson & Poole, 1982: 5 seconds for marmosets, Govindarajulu et al., 1993: no interval for vervet monkeys), but the most common one is 10 seconds (Cordoni et al., 2016; De Oliveira et al., 2003; Iki & Hasegawa, 2020; Mackey et al., 2014; R. Wright et al., 2018), which we also chose for our study. Additionally, if the play partners changed or if one other player joined, we considered that the play bout had ended, even if the play elements were less than 10 seconds apart. We considered the arrival of a new player as a new play bout. Besides following the published literature we additionally explored how changing the intervals between play elements would affect the resulting amount of time playing (see this additional analysis in section S1), which corroborated our decision to adopt a 10 second interval.

Based on these calculated play bouts we calculated the proportion of time a dyad or triad was observed playing out of the total time observed in a specific coded session. The dyads were specified as either $Dyads_{PARENT\text{-}IMMATURE}$ (where we added all the $Dyads_{MOTHER\text{-}IMMATURE}$ and $Dyads_{FATHER\text{-}IMMATURE}$ together) or $Dyads_{TWINS}$. The triads were specified as $Triads_{PARENT\text{-}TWINS}$ (where we added all the $Triads_{MOTHER\text{-}TWINS}$ and $Triads_{FATHER\text{-}TWINS}$ together). We adjusted for the time a dyad or triad could have been playing but one of the individuals was out of sight by subtracting from the total time observed the time when at least one individual was out of sight.

The play compositions were calculated as follow :

$\mathbf{Dyads_{PARENT\text{-}IMMATURE}}$ = Time $_{\text{either infant play} \cap \text{mother play}}$ + Time $_{\text{either infant play} \cap \text{father play} +}$ / (2 * Total Time $_{\text{TIME OBSERVED - OOS}}$)

$\mathbf{Dyads_{TWINS}}$ = Time $_{\text{infant play} \cap \text{infant play}}$ / (Total Time $_{\text{TIME OBSERVED - OOS}}$))

$\mathbf{Triads_{PARENT\text{-}TWINS}}$ = (Time $_{\text{infant play} \cap \text{infant play} \cap \text{mother play}}$ + Time $_{\text{infant play} \cap \text{infant play} \cap \text{father play}}$) / (Total Time $_{\text{TIME OBSERVED - OOS}}$)

Part 3: Parental investment

We compared female to male breeders' investment in play by calculating the $Play_{MOTHER\text{-}IMMATURE}$ and $Play_{FATHER\text{-}IMMATURE,}$ as proportions of time spent playing respectively by the female breeder and the male breeder with one (dyad) or two immatures (triad), out of the total time observed in a specific session. We adjusted for the time a breeder or immature could have been playing but was out of sight by subtracting from the total time observed the time when at least one individual was out of sight.

We additionally determined the predicted probability of simultaneous play of both parents under the assumption that play bouts happen independently: $P_{MOTHER\ PLAY} \times P_{FATHER\ PLAY}$ = $Time_{MOTHER\ PLAY}$ / (Total Time $_{\text{TIME OBSERVED - OOS}}$) × $Time_{FATHER\ PLAY}$ / (Total Time $_{\text{TIME OBSERVED - OOS}}$) and the observed probability: Time $_{\text{Aplay} \cap \text{Bplay}}$ / (Total Time $_{\text{TIME OBSERVED - OOS}}$) for each session.

If the observed probability of simultaneous play is lower than the predicted probability, individuals take turns playing, if the opposite is true, individuals are more likely to play synchronously.

We calculated the food sharing rate as the number of crickets reactively or proactively given over the total number of trials per month of the immatures' life.

We calculated the carrying rate as the number of immatures carried i.e., we summed up the number of immatures, maximum 2, on every hourly scan, in total over the 120 days of carrying data collection controlling for the number of immatures the focal parent could have carried controlling for the times where no data was available i.e., missing data in the hourly scans.

Data analysis and statistics

All statistical analyses were conducted using the statistical software R studio (2023.12.1). We used a Generalized Linear model (GLM, package "stats") and zero inflated Generalized Additive Models for Location, Scale and Shape (package 'Gamlss'). Our outcome variable for model 1 is a discrete proportion (number of social, L/R or object elements over the total time observed in a specific session controlled for the time out of sight), we therefore chose to use a model from the poisson family. For models 2, 3a and 3b, our outcomes are continuous proportions (time spent playing over total time observed controlled for time out of sight), we thus used a model from the zero-inflated beta family.

We controlled for overdispersion in the Poisson GLM and adjusted accordingly by fitting a quasi-poisson. For the poisson GLM, we controlled for the absence of outliers (standardized residuals < 3), high leverage points (hat values < 3 * mean hat value) and influential cases (cook's distance < 1).

The homogeneity of the residuals was assessed by inspecting residual plots for all models (function 'plot' and function 'resid_plots', package 'gamlss.ggplots'). Worm plots were used for the Gamlss models .

We controlled for the absence of collinearity between the predictors (function 'vif') for all models.

The full models including all relevant predictor variables were always compared to the null models only including the intercept by using a likelihood ratio test (functions 'anova'; package 'car' and function 'lrtest'; package 'lmtest'). Model selection was based on the Akaike Information Criterion AIC. Post hoc comparisons were conducted on the full model (function "emmeans" and "emtrends", package "emmeans"). We report the overall goodness-of fit of the models with conditional R2 values (function "r.squaredGLMM", package "MuMIn" and function 'Rsq', package 'gamlss'). Prediction plots were drawn using the functions 'Effect' (package 'effects'), 'ggplot' (package 'ggplot2') and 'predict_response' (package 'ggeffects').

Part 1: Play trajectories

Our first analysis modelled the occurrence per coded session of play elements categorised as 'social', 'object manipulation' or 'L/R'. For social play, all play elements were counted indiscriminately, without taking into account the play composition (dyads or triads) in which they took place. The number of elements from each category was summed up per coded session (Poisson GLM, model 1). We controlled for the relative length of the coded session by setting the logarithm of the total observed time for the coded session in question, adjusted with the time out of sight as the offset,. We included the play category (social, object, L/R), the age of the immatures (in weeks) and the group as well as all two-way interactions between play category and age of the immatures, as fixed effects. We set a planned contrast between the different categories of play, with the first contrast being social play against the two others categories and the second contrast comparing object versus L/R play.

Part 2: Partner preference

Our second analysis allowed us to investigate the immatures' favourite partner. We calculated the proportion of dyadic and triadic play to compare parent-immature play to twin play as our outcome in a zero inflated Generalized Additive Model for Location, Scale and Shape (Gamlss, model 2). We included the play composition ($Dyads_{PARENT\text{-}IMMATURE}$, $Dyads_{TWINS}$, $Triads_{PARENT\text{-}TWINS}$), the age of the immatures (in weeks) and the group as well as the two-way interaction between dyad identity and age as fixed effects. We set a planned contrast between the different play compositions, with the first contrast being dyadic (both $Dyads_{PARENT\text{-}IMMATURE}$ and $Dyads_{TWINS}$) against triadic play and the second contrast comparing the $Dyads_{PARENT\text{-}IMMATURE}$ to the $Dyads_{TWINS}$).

Part 3: Parental investment

To understand if mothers and fathers would play differently, we calculated the proportion of time they spent playing per coded session as our outcome and fitted a zero inflated Generalized Additive Model for Location, Scale and Shape (Gamlss, model 3a). Breeder sex (male, female), age of the immatures (in months) and group identity were used as fixed effects.

We then examined whether and how much the father and the mother played simultaneously. We used a paired Wilcoxon signed rank test (function 'wilcox.test', package stats) to compare the predicted probability of overlap to the observed probability.

Additionally, we analysed whether there were other factors than breeder sex that could influence the involvement in play behaviour. To do so we ran another model (Gamlss, model 3b) with carrying rate, food sharing proportion, age of the immatures (in months) and group identity as fixed effects.

Results

Part 1: Play trajectories

We first analysed the developmental trajectories of the three play categories (L/R play, object manipulation and social play). The full model (AIC = 988) that included the fixed effects play category, age of the immatures and group as well as the two-way interactions between age and play category, explained the data significantly better than the null model (N_{total} = 63 , $N_{individuals}$ = 6, N_{groups} = 3; AIC = 3278; likelihood ratio test: X^2 (7) = 2303, $p < 0.001$). We found that immature marmosets did increase their amount of social play with age. There was a very low and homogeneous proportion of both object manipulation and L/R play throughout the 5 months of observations (Figure 2). Further, social play was indeed the most prominent form of play (see Table 2 for model summary).

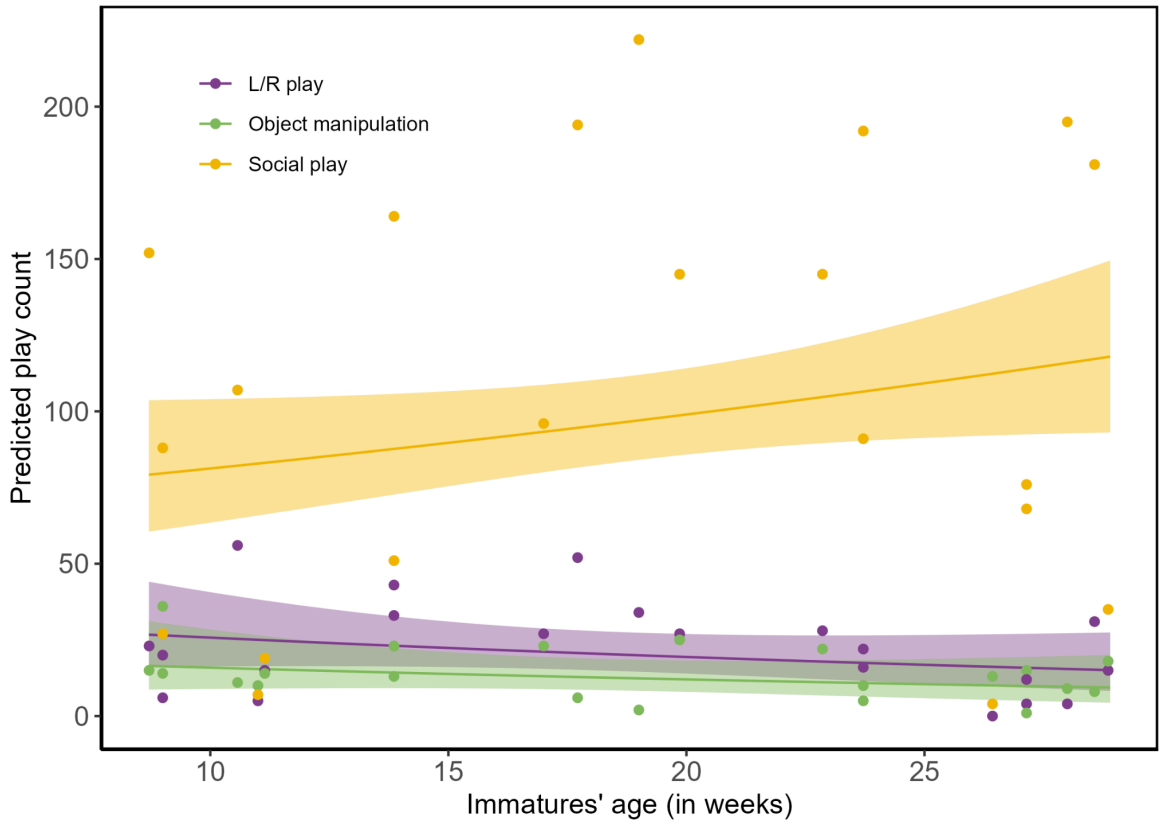

Figure 2. Predicted trajectories of the three play categories between 2 and 6 months old. Each point represents the frequency of a specific play category of a pair of twins from the same group (N_{total} = 63, N_{twins} = 3 pairs of twins, N_{groups} = 3). Shaded areas illustrate 95% confidence intervals. Raw data are shown as points. Points are raw counts of play elements in a single session without accounting for session duration and time out of sight.

Part 2 : Partner preference

Next our focus was on immatures' favourite play partners, i.e., did they prefer to play. with the twin (dyad), with a parent (dyad) or with the twin and a parent (triad). The full model (AIC= –148.55) that included the fixed effects play composition, age of the immatures and group as well as the two-way interactions between age and play composition, explained the data significantly better than the null

model (N_{total} = 63, $N_{individuals}$ = 12, N_{groups} = 3; AIC = –126.79; likelihood ratio test: X^2 (7) = 35.77, p < 0.0001).

We found a significant interaction between play partner composition (i.e.,$Dyads_{PARENT\text{-}IMMATURE}$, $Dyads_{TWINS}$ and $Triads_{PARENT\text{-}TWINS}$) and age of immatures. Planned contrasts showed that with immature age the odds of playing in a dyad composed of two immatures ($Dyads_{TWINS}$) increased 5% faster compared to a dyad composed of a parent and an immature ($Dyads_{PARENT\text{-}IMMATURE}$). No difference was found between the dyadic and triadic play in terms of rate of change with immature age (Table 2, model 2, Figure 3a).

On average, between 8 weeks old until 19 weeks old, an immature (independent of group identity) played in a dyad with one of their parents for 54% out of the total time spent playing in dyads.Then between 19 weeks until 29 weeks old, immatures played on average 29% of the time with one of their parents. This was led by an increase of play between twins ($Dyads_{TWINS}$) and not a decrease in parent-immature ($Dyads_{PARENT\text{-}IMMATURE}$) play.

In addition we found differences between the groups in the proportion of time spent playing overall (indifferent of the play composition) and post hoc tests identified the group “Jambi” as playing less compared to the group “Guapa” and “Washington” (see Figure S2, Table S3).

Part 3: Parental investment

Thirdly investigated the difference in amounts of play between fathers and mothers. The model (AIC= –51.8353) including the sex of the parent, the age of the infants (in months) and group identity did not explain the time spent playing better than the null model (AIC= –53.0186). Contrary to our predictions, mothers and fathers played at equal amounts throughout the five months of observation (see Table 2, model 3a, Figure S3).

In addition, we wanted to quantify if and how much time parents played simultaneously either in triad or tetrad (mother-father-immature(s)), in two simultaneous dyads (father-immature and mother-immature) or with each other (father-mother). We examined all coded data and found a total of 6,43 seconds of overlap (over 1060 minutes of observation), equalling 0,0001 % of observation time. The paired Wilcoxon signed rank test showed that there was a significant difference (z [20] = 3.41 ; p <0,001, r = –0.74) between the predicted and observed simultaneous play from the father and the mother, with lower observed values of simultaneous play than predicted values (Figure 3b).

Lastly we examined the trade-offs between playing and other care-taking behaviours. The model (AIC = –55.4965) including carrying rate, food sharing proportion, age of the infants in months and group identity did explain play involvement better than the null model (AIC= –53.0186), however this was driven by the group identity and not carrying or food sharing (see Table 2, model 3b).

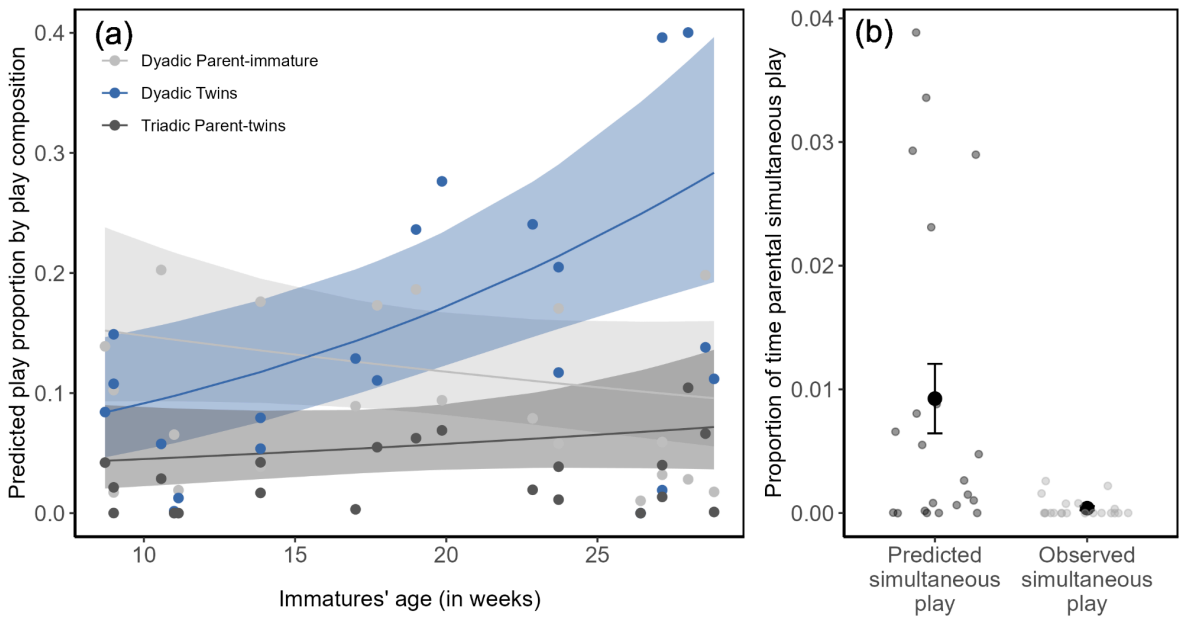

Figure 3. Partner preference and simultaneous parents play. (a) Predicted proportion of time spent playing in the different compositions over the 5 months of observation (model 2). Shaded areas illustrate 95% confidence intervals. Raw data are shown as points. A point represents the play proportion of a specific composition (i.e.,$Dyads_{PARENT\text{-}IMMATURE}$, $Dyads_{TWINS}$ and $Triads_{PARENT\text{-}TWINS}$) in a single session ($N_{total}$ = 63, $N_{individuals}$ = 12, N_{groups} = 3). (b) Comparison between predicted and observed proportion of time individuals played simultaneously (N_{total} = 42, $N_{individuals}$ = 6, N_{groups} = 3). Points represent the raw values of predicted (black) and observed (grey) simultaneous play per session. Error bars are based on raw data and show the standard error of the mean, the mean is represented with the opaque black dot.

Table 2. Summary of the GLM model 1 and Gamlss models 2 and 3. Bold values indicate significant predictors ($p < 0.05$)

Dependent variable	Fixed factors	estimate (s.e.)	Odds ratio	95% CI	tvalue	P
model 1: Play trajectory: R^2_μ = 0.18						
Play element counts	Intercept	-2.73 (0.25)	0.07	0.039; 0.106	-10.79	**3.4e-15**
	social play versus L/R and object play	0.3 (0.13)	1.36	1.045; 1.774	2.26	0.03
	L/R play versus object play	-0.24 (0.34)	0.78	0.396; 1.518	-0.72	0.48
	Immatures' age (in weeks)	-0.012 (0.013)	0.99	0.964; 1.012	-0.97	0.34
	Jambi group	-0.21 (0.15)	0.81	0.597; 1.096	-1.35	0.18
	Washington group	0.026 (0.14)	1.03	0.778; 1.353	0.18	0.85
	social play versus L/R and object play * age	0.016 (0.007)	1.02	1.002; 1.03	2.29	**0.03**
	L/R play versus object play * age	0.00026 (0.018)	1.00	0.965; 1.037	0.01	0.99
model 2: Partner preferences: R^2_μ = 0.43						
Play proportion by play composition	(Intercept)	-2.61 (0.3)	0.07	0.0405; 0.134	-8.58	**1.30E-11**
	Triadic versus dyadic play	0.35 (0.22)	1.42	0.926; 2.19	1.61	0.11
	Dyadic parent-immature versus twins	-0.77 (0.3)	0.47	0.259; 0.834	-2.57	**0.013**

	Immatures' age (in weeks)	0.024 (0.013)	1.03	0.998; 1.05	1.84	0.071
	Family group (Jambis)	-0.79 (0.24)	0.46	0.284; 0.731	-3.26	**0.002**
	Family group (Washingtons)	-0.12 (0.22)	0.88	0.576; 1.36	-0.57	0.57
	Triadic versus dyadic play * age	-0.00097 (0.01)	1.00	0.979; 1.02	-0.09	0.93
	Dyadic parent-immature versus twins * age	0.049 (0.015)	1.05	1.02; 1.08	3.41	**<0.01**
model 3a: Parental play investment: R^2_μ = 0.065						
Parent play proportion	(Intercept)	-1.91 (0.32)	0.15	0.080; 0.28	-5.99	**6.59E-07**
	Parent's sex (mother)	-0.46 (0.28)	0.63	0.37; 1.09	-1.64	0.11
	Immatures' age (in months)	0.048 (0.083)	1.05	0.89; 1.2	0.57	0.57
model 3b: Caretaking and play: R^2_μ = 0.26						
Parent play proportion	(Intercept)	-2.1 (0.52)	0.12	0.044; 0.341	-4.02	**<0.001**
	Immatures' age (in months)	0.027 (0.09)	1.03	0.862; 1.222	0.30	0.77
	Family group (Jambis)	-1.07 (0.35)	0.34	0.174; 0.672	-3.11	**<0.01**
	Family group (Washingtons)	-0.65 (0.34)	0.52	0.268; 1.012	-1.92	0.06
	carrying rate	1.04 (2.12)	2.84	0.0449; 179	0.49	0.63
	Food sharing proportion	0.48 (0.73)	1.62	0.389; 6.711	0.66	0.51

Discussion

In this study we investigated the ontogeny of play in three groups (N = 12) of cooperatively breeding common marmosets with infants between the age of two to six months. We found that the trajectories of social, L/R and object play follow the expected pattern with an increase in social play over the observed months and a very low and unchanging frequency of object and L/R play. Infants' partner preference changed depending on their age, with the twin becoming the more important play partner over time but adult play remaining similarly important (of the total when an immature played with a partner, this partner was in 54% of the time a parent during weeks 4 to 19 weeks old, and in 29% during weeks 19 weeks old to 29). Lastly we did not find any differences in parental investment into play between mothers and fathers and indeed also did not find any support for trade-offs between other care-taking behaviours (such as food sharing or carrying) and play. However, we found strong evidence that parents avoided playing at the same time.

Part 1: Play trajectories. The social play trajectory followed the expected pattern, with an increase of play frequency over the five months of observation. Since the peak of play is expected at the juvenile period, as in many other species where play has been researched (e.g. dogs (Pal, 2010), jungle babblers Turdoides striatus (Bond & Diamond, 2003; Gaston, 1977), gazelles Gazella cuvieri (Gomendio, 1988), and marmosets are considered juveniles between 3 months (Abbott et al., 2003) and 12 months old, it is unsurprising that the decrease in social play frequency was not yet observed in our observation period which ended at 6 months of age.

We also confirmed that the different play categories are not equally distributed. Social play was much more common than L/R play and object manipulation throughout the five months of observation. This pattern is consistent with the social niche of marmosets that heavily relies on others for many of their daily activities (Burkart et al., 2022; Koenig, 1998; Yamamoto & O.Box, 1997), but do not have to train any particular technical skills, especially for tool use (Schiel & Souto, 2017). This echoes the

findings in bonobos and chimpanzees where the former played far less with objects than the latter (Kenward et al., 2011; Koops et al., 2015), which is mirroring the tool use propensities of the two species. Our results provide support for the hypothesis that object play may be a developmental precursor to complex, flexible tool use (Montgomery, 2014).

Until one month old, marmosets are not independent and are carried by their parents or helpers (Abbott et al., 2003). They can still be carried between one and two months as well, more or less frequently and they are still learning how to walk during this period (Schultz-Darken et al., 2016). Here, we thus witnessed the very beginning of social play in an infant's life. Due to the lower mobility during the first and second month of an infant's life it is possible that object manipulation was more prominent within this short time period, where they are not ready to start playing socially but would be able to interact with objects. Further analyses of the time window between birth and two months would be required to better understand the developmental trajectory of object play and if the low frequency observed here would also hold earlier in development.

Regarding the other form of solitary play i.e., L/R play, the same reasoning applies and further research would need to explore how this behaviour develops between birth and two months. However, infant marmosets are just learning to walk between one and two months whereas L/R play requires a certain control of motor capacities, it is thus surprising to see such a low frequency of this behaviour between two and six months old. One main issue with coding L/R play is that it is very difficult to disentangle from mere locomotion. If an individual is running, with no play face (the play face is seen more often in social play than solitary play (Ross et al., 2014) and alone, this individual is assumed to "just" move and not play, but a chance remains that the individual indeed was playing (for an in-depth discussion of reasons why solitary play is especially difficult to code, regarding the criteria established by Burghard, 2005 see section S2).

Part 2: Partner Preference. We then investigated the immature play partner preferences. As predicted, twin play increased with age, but the decrease expected in parent-immature play was not observed, perhaps because again similar to the results in part one, this happens later in development during the juvenile period. Data on a larger sample size with older immatures would therefore be required to fully capture the development of partner preference over time in callitrichidae.

Our results also showed that parents were important partners during playful interactions throughout the observation period, despite the constant availability of a same-aged partner (the twin). This contrasts with what has been observed in squirrel monkeys Saimiri boliviensis (Biben, 1998), for which the low involvement of the mothers has been attributed to the presence of peers, with the underlying idea that play would cost mothers energy and time that they might not be able to afford. Similar patterns of a strong preference of immatures to play with individuals as close as possible in age, at any age observed, have been reported in tamarins (Kostan & Snowdon, 2002; Epple & Katz, 1980), meerkats Suricata suricatta (Sharpe, 2005) and Gorillas Gorilla gorilla (Maestripieri & Ross, 2004). One possible explanation for such high levels of parental involvement in play could be the captive housing condition reducing the energy demands on parents and thus allowing them to play more. What speaks against this argument is that other studies conducted in captivity have not found that parents are more involved in play e.g., hyaenas Crocuta crocuta (Drea et al., 1996), Gorillas (Maestripieri & Ross, 2004).

It is important to note that the groups included in the sample for this study did not include any helpers thus very likely the amount of mixed-age play is underestimated, as the majority of studies in callitrichids show more play by juvenile and subadult helpers than breeders (Cleveland & Snowdon, 1984; De Oliveira et al., 2003; Stevenson & Poole, 1982). Cooperation is key in marmosets amongst all family members and one hypothesis about the function of play is that it might enhance social skills. Our results combined with the evidence from other research on callitrichids support this notion especially since cooperative acts do not only happen among peers in callitrichid groups but all group members (Burkart et al., 2009). Furthermore a recent study investigated the social function of play signals in the same groups of common marmosets. Results showed that marmosets use body posture as a multi-functional signal to initiate and prolong their play interaction, as well as allowing for more intense play (Adriaense et al., in prep), showing how communication is key during play interactions.

Lastly, group identity seemed to have had an important impact on how much an individual played, for the immatures as well as for the parents. All individuals in the Jambi group played less than the individuals in the Guapa group, raising the question as to whether different amounts of play are part of "group personalities" in playfulness. Previous research on marmosets has shown group-level similarities (i.e., "group personalities") on traits such as boldness and exploration (Koski & Burkart, 2015). These traits were better explained by social mechanisms (social proximity within the group) than genetic relatedness between individuals. To strengthen the hypothesis that playfulness is a group personality trait and to understand how flexible this trait is, the study of more groups would be required as well as the monitoring of those group members over time and the changes in playfulness or not when individuals change group to form a new family.

Part 3: Parental investment. Finally, we explored the difference of play investment between mothers and fathers, as well as the impact of parental investment measures i.e., food sharing and carrying, regardless of the sex of the parent on time spent playing. We found that there was no significant difference between mothers and fathers with regard to the time they spent playing with their infants. In the species where parents do get involved in playful interactions, especially at a young age, these playful interactions are often exhibited with the primary caregiver i.e., mothers in chimpanzees Pan troglodytes (Pellegrini & Smith, 2005) or orangutans Pongo spp (Kunz et al., 2024). In species where males take an active role in immatures caretaking, they also show an important involvement in playful interactions, sometimes more than the mothers: In horses, stallions are the preferred play partners compared to the mothers and they also actively seek playful contact with their foals in contrast to the mothers (Šandlová et al., 2020). In Javan gibbons Hylobates moloch, fathers play more and groom the infants more than mothers do (Yi et al., 2023). In humans, who are cooperative breeders as the common marmosets, even if there is no final consensus on the comparison of father-child/mother-child play frequency (Amodia-Bidakowska et al., 2020) it is clear that both parents are very involved in playful interactions (Smith & StGeorge, 2023). Some studies even found play to be equally distributed amongst parents (Laflamme et al., 2002). In addition, Amodia-Bidakowska et al. (2020) also found that investment in play behaviours was dependent on parental employment status, thus dependent on the time available to allocate to play behaviour. Therefore, it makes sense that in a cooperative species, both parents share the playful activities with their offspring.

On the other hand it would be expected that energetic constraints might factor into the decision of how much time is spent playing. Our result is therefore surprising as we expected the parent with

more energetic constraints, i.e. the mothers, to play less compared to fathers. Parenthood is indeed more demanding for the mothers, for one part because of the twin pregnancy, for another part because of high lactation costs associated with twin care (Schiel & Souto, 2017), as well as because of postpartum oestrus (Beehner & Lu, 2013; Leutenegger, 1973). There was also no effect of age on time spent playing for either of the parents. This could indicate that the decrease in parental play happens later in development and thus that this difference between mothers and fathers only arises later on. The group's composition could also explain why both parents were equally involved in playful sessions as the lack of helpers could have led parents' to share the play "duties". Helpers are usually older brothers and sisters and that would make them appealing play partners for the immatures. It would be interesting to compare with groups having helpers to see if the parents indeed compensate for the lack of help when there is none or if this is a normal situation for the parents to play this much with their offspring. For other behaviours involving the immatures' such as carrying them or sharing food with them, the parents' involvement is dependent on the help they receive from helpers and especially from male helpers, we would expect play behaviour to also follow this rule (Burkart, 2015; Snowdon & Ziegler, 2007).

Intriguingly, there were almost no occasions in 1060 minutes of observation time, where both parents played simultaneously, it was always either the father or the mother with the infants. The fact that they alternated who was playing with the infants could have two explanations. The first is that adults do not often play together in general, in all species where we know play exists (Palagi, 2023; Pellis & Iwaniuk, 2000), likely in part to avoid the risk of escalation into real fights. In highly socially tolerant callitrichids this explanation is unlikely as in bigger groups with only adults play between adults still occurs (personal observation in wild common marmosets by J.M.B.). The second explanation is linked to the potential threat individuals face while playing. Play can be costly for small prey animals because vigilance and play are hardly possible at the same time (Beauchamp 2015; Biben, 1998; Harcourt, 1991; Hausfater, 1976), since both require the attention of the player. If both parents would play at the same time, that would make infants very vulnerable to predators, especially in small groups such as the ones included in this sample. This alternation between parents appears to be similar to the coordination capacity that marmosets show in a different context, namely when coordinating being vigilant and feeding head-down, in a situation where both of these behaviours are mutually exclusive (Brügger et al., 2023; Phaniraj et al., 2023). In a study on golden lion tamarins, De Oliveira et al. (2003) showed that adult breeders increase their vigilance when immatures are playing. This would hint again at the fact that adults do avoid playing together to make sure at least one individual can be vigilant in this dangerous context.

Since there was no impact of the parents' sex on play investment, we checked whether a difference would arise at the individual level depending on how those individuals were involved in infant care taking. But neither carrying nor food sharing were predictive of how much an individual would play with his or her offspring, showing that play might be a special form of parent-offspring interaction or that our sample simply lacks statistical power to show this trade-off.

This study shows the clear preference cooperatively breeding common marmosets exhibited for social play that increases with age over months two to six of their development. More importantly it highlights the large and similar involvement of both parents in play even though same aged twins and thus a peer to play would always be available. We do not find any support for trade-offs between other care-giving behaviours and play. Besides showing general patterns of immature play in this

species we provide a detailed illustrated ethogram of the observed play behaviours with accompanying supplementary video material of all coded play behaviours encouraging future research on this highly dynamic behaviour in this species.

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