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Behaviour (2021) DOI:10.1163/1568539X-bja10074

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Comments/Reflections

Swimming and diving as social play in juvenile rhesus macaques (*Macaca mulatta*)

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Received 15 September 2020; initial decision 16 October 2020; revised 17 December 2020; accepted 8 February 2021

Abstract
Although play is ubiquitous throughout the animal kingdom, and in primates especially, the ultimate explanations and proximate mechanisms of play are not well understood. Previous research proposes that primate play may be important for the development of cognitive skills including executive function, emotional regulation, and impulse control, and could help to build social skills and network connections needed in later life. However, many of these hypotheses have not been thoroughly tested. Here, we report observations of novel play behaviour that could provide unique opportunities to explore these hypotheses: young rhesus macaques (*Macaca mulatta*) engaging in aquatic social play in a naturalistic setting. Based on our observations, we propose that aquatic play has social elements that make it ideal for testing ultimate explanations of primate play and hypotheses about the cognitive mechanisms that support it.

Keywords
play, non-human primates, development, social behaviour, cognition, joint activities.

1. Introduction

Play is widespread across mammals, but is particularly evident in the primate order (Vandenberg, 1978). Primates are highly social mammals often with complex social organizations and structures (Clutton-Brock & Harvey, 1977; Cheney et al., 1986; Kappeler & van Schaik, 2002), so it is perhaps unsurprising that play is a well-documented aspect of primate sociality (Poirier &

Smith, 1974; Palagi et al., 2016; Palagi, 2018). While difficult to precisely define, Burghardt's (2005) five criteria have been widely used to identify play (e.g., Graham, 2011; Palagi et al., 2016; Costa et al., 2019). According to these criteria, play is behaviour that: (1) does not contribute to current survival, (2) is spontaneous, intentional, and rewarding, (3) can be awkward or precocious, (4) is often repeated but not stereotyped, and (5) is initiated when relatively free from stressors.

Scientists have proposed many hypotheses to explain the ubiquity of social play across primates (Poirier & Smith, 1974; Yanagi & Berman, 2017; Palagi, 2018). As social play has been observed primarily in juveniles (Fagen, 2002), some hypotheses propose that play serves a developmental function because play incurs energetic costs, risks escalation to aggression (Palagi et al., 2016; Yanagi & Berman, 2017), and often requires differing roles (e.g., attacker and defender; Pellis & Pellis, 1996). Thus in play, juveniles practice self-regulation and communicative signalling skills (Pellis & Pellis, 1996). As social play introduces uncertainty relative to ritualized behaviours (Burghardt, 2017), it may promote behavioural innovation and set the stage for adult social competence via trial-and-error learning (Poirier & Smith, 1974; Palagi, 2018). Similarly, researchers have noted links between social play and both brain size/growth and behavioural flexibility (Graham, 2011; Montgomery, 2014), as well as between brain size and executive function in adulthood (MacLean et al., 2014). For example, social integration, the maintenance of dominance hierarchies and group structure, and effective social communication in adulthood may be aided by the development of social-communicative skills requisite of avoiding aggression during social play in juvenile life (Poirier & Smith, 1974; Palagi, 2018).

Scholars outside of animal behaviour have categorized play behaviour according to its sociality, especially in humans. In a seminal study of preschool children, Parten (1933) distinguished between three types of social play: (1) parallel play, which is independent play among others in a similar manner but without attempted influence of others' play (e.g., playing "beside" rather than "with" others), (2) associative play, where participants act similarly or identically in a common activity but with no organization around or subordination to a common/shared goal, and (3) cooperative play, which is purposefully organized around a shared goal and necessitates distinct, complementary roles. Where non-human primate social play falls along this human-centered continuum remains an open question, with

some comparative researchers arguing that shared goals and intentions may be uniquely human phenomena (Tomasello & Carpenter, 2007; Tomasello & Moll, 2010; Tomasello et al., 2012). However, other researchers have argued that these abilities are unlikely to be human-unique based on observational studies of non-human primate social play (Gómez, 2010; Tanner & Byrne, 2010). Research into the intricacies of non-human primate social play could therefore provide novel opportunities to empirically test for the human uniqueness of cognitive mechanisms that facilitate mental state representation and sharing (Heesen et al., 2017).

Here, we document observations of primarily juvenile rhesus macaques (*Macaca mulatta*) at the Cayo Santiago Biological Field Station (see Table A1 in the Appendix). The field station is a small island (34 acres) off the east coast of Puerto Rico, and is home to approximately 1700 free-ranging rhesus monkeys (Kessler & Rawlins, 2016). The population is diverse in terms of age, sex, and social rank, and individuals interact in both inter- and intra-group settings, making it ideal for studying social behaviour in a naturalistic setting (Maestripieri & Hoffman, 2012). While play on Cayo Santiago has been well-documented in the field station's 80-year history, most work has focused on terrestrial social play (Breuggeman, 1978; Yanagi & Berman, 2014a,b, 2017). Terrestrial play typically consists of physical contact between individuals with facial and bodily expressions that help to solicit and facilitate playful (as opposed to antagonistic) interactions (Yanagi & Berman, 2014a,b). Below, we note similar patterns in a heretofore understudied form of aquatic play.

2. Swimming and diving as social play

The handful of existing studies examining how young rhesus macaques interact in an aquatic environment were conducted in a laboratory setting. In these studies, swimming behaviour was largely independent and elicited via a food reward rather than occurring spontaneously (Anderson et al., 1992, 1994). To our knowledge, only one article to date has described aquatic play behaviour among the monkeys on Cayo Santiago. In New Scientist, Berman (1977) detailed a mixed-age group of monkeys swimming off the island's coast. While Berman's (1977) account described juvenile diving behaviour and interactions between infants and mothers, we focus specifically on social play among juvenile peer groups. Berman (1977) observed that juveniles

appeared more independent and less risk-averse than infants or older groupmates, diving into shallow (<60 cm) water from branches three to seven meters high. Infants waded in shallow water, but stayed near their mothers. Berman suggested that aquatic play may aid in social development, facilitate physical and sensory development, or promote temperature regulation or parasite removal (Berman, 1977).

Our observations focus on the social, peer-directed interaction evident in monkeys' swimming and diving behaviours. As a guide, we used a systematic analysis of terrestrial rhesus macaque play to identify similar patterns in our observations (Yanagi & Berman, 2014a; see also Table A2 in the Appendix). Yanagi & Berman (2014a) identified two indicators of play: play signalling and play behaviours. Play signalling refers to facial expressions or body postures used to indicate to a conspecific that one's subsequent actions are not aggressive in nature. In rhesus macaques, these can include a relaxed open-mouthed facial expression (i.e., the 'play face'), but also more subtle expressions such as the gait of their walk (i.e., gamboling). As compared to play signals, play behaviours are more overt, and typically involve physical contact between two individuals as in the case of wrestling, or rough-and-tumble play, where individuals grasp, push, and pull each other (Yanagi & Berman, 2014a).

3. Results

On multiple occasions (see Table A1 in the Appendix and the Videos 11 July 2015 0:00:01,10, 10 June 2016 00:04:04,11 at 10.6084/m9.figshare.13796546), we observed groups of juvenile monkeys gather around one of many shallow pools surrounded by trees and other brush (e.g., Figure 1). Individuals climbed the surrounding vegetation, generally pausing three to seven meters above the water as Berman noted (Berman, 1977). Interestingly, individuals dove off their branches into the water such that two individuals rarely jumped concurrently (Video 10 June 2016 00:04:04,11 at 10.6084/m9.figshare.13796546). Before jumping, individuals watched groupmates dive and swim to shore (Figures 2 and 3) and wrestled with and shoved individuals in the branches above the water (Figure 4). These behaviours were accompanied by facial expressions (e.g., open-mouth play face, Figure 4) and body postures (e.g., 'dangle and stare', Figure 4) thought to solicit, facilitate, and maintain play (Symons, 1974; Yanagi & Berman, 2014b).

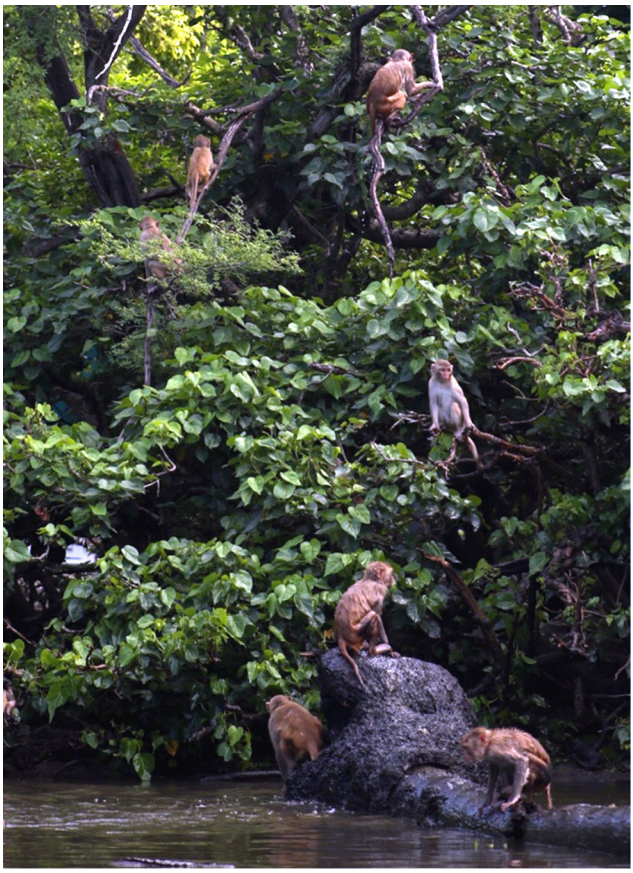

Figure 1. A group of juvenile rhesus monkeys gather around an inland shallow (<30 cm) pool of collected rainwater at the Cayo Santiago Biological Field Station.

We observed play signals and play behaviours when individuals were in the water, as individuals could be seen gamboling towards one another (Video 15 July 2015, 00:47,05; 00:59,46 at 10.6084/m9.figshare.13796546), and wrestling (Figures 4 and 5), chasing (Video 15 July 2015, 01:01,12 at 10.6084/m9.figshare.13796546), slapping (Figure 6) and cuddling (Figure 7). Therefore, swimming and diving appeared to constitute social play in which individuals exhibited some sensitivity to groupmates' actions in modulating their behaviour.

Other researchers have noted additional play signals and behaviours in a terrestrial setting which we did not observe. For instance, Yanagi & Berman

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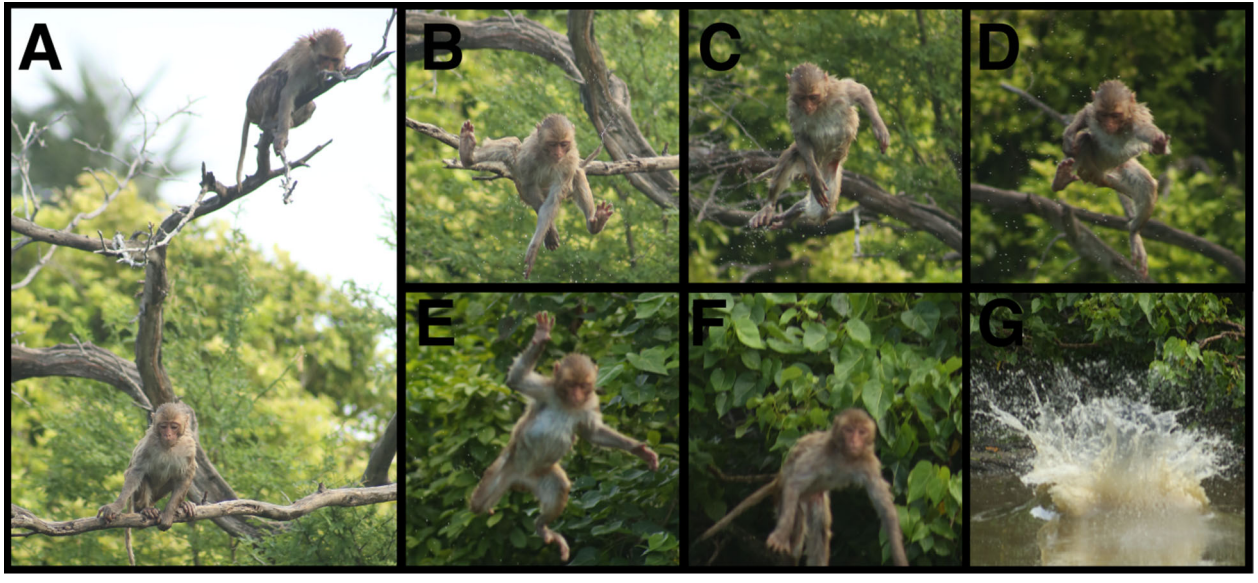

Figure 2. On its surface, the rhesus monkeys' diving behaviour appeared to be a solitary act. However, in almost every instance of diving behaviour that we witnessed, conspecifics watched and waited to dive (e.g., panel A). Here, a male dives (foreground panel A; panels B–G) while another male juvenile looks on (background right, panel A).

Figure 3. Juvenile rhesus monkeys appear to take turns when diving from branches two to three meters above the water, and conspecific peers watch individuals from other branches. Here, a male juvenile jumps while two male juveniles watch.

(2014a) identified 'crouch and stare' signalling in which an individual lowers its ventral side to the ground and stares at a conspecific, and the 'leg peek' in which an individual looks back at a conspecific through its legs. Both were noted as important signals in terrestrial play behaviour, but we did not witness these behaviours in any instances of aquatic play (however, both signals would of course be difficult to perform in an aquatic setting). We also witnessed aquatic play behaviours that would be impossible in the absence of water; for instance, individuals diving from branches (Figures 2 and 3; Video 11 July 2015, 00:02,02; 10 June 2016 04:05,00 at 10.6084/m9.figshare.13796546) or swimming beneath the surface of the water (Video 15 June 2015, 00:49,08; 01:19,04 at 10.6084/m9.figshare.13796546). Finally, we observed some behaviours that may have been adapted for the water from terrestrial social play. For example, Yanagi & Berman (2014a) noted "chasing" as a play behaviour, which may include one individual running after, jumping, or climbing towards another. In our observations, we noted individuals lunging towards one another in the water (Figure 6) and swimming after one another (Video 15 July 2015, 01:01,12 at 10.6084/m9.figshare.13796546). Taken together, we observed both similarities and differences between the ways social play was realized in an aquatic setting relative to

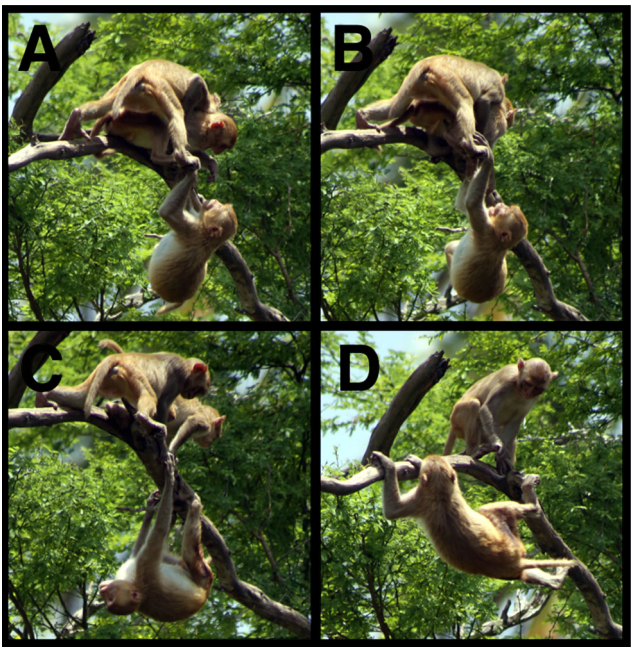

Figure 4. Many of the interactions in and around the water were accompanied by play signals common in terrestrial play. Pictured here are three rhesus monkeys wrestling in branches above the water; the juveniles exhibited play signals both facial and postural; in panels A and B juveniles with a "play face" expression; in panel C a "dangle and stare" posture.

previous descriptions of terrestrial social play, and some of our observations suggest that terrestrial play behaviours may be adapted to aquatic settings (for more behaviours and definitions, see Table A2 in the Appendix).

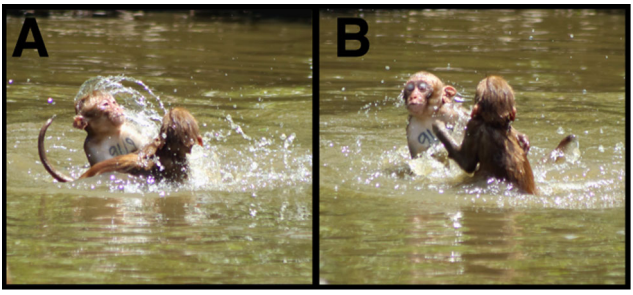

Figure 5. In addition to the diving behaviour we witnessed, many of the juveniles also engaged in play behaviour above and in the water after diving. Here, two juvenile monkeys wrestle in the water below the branches.

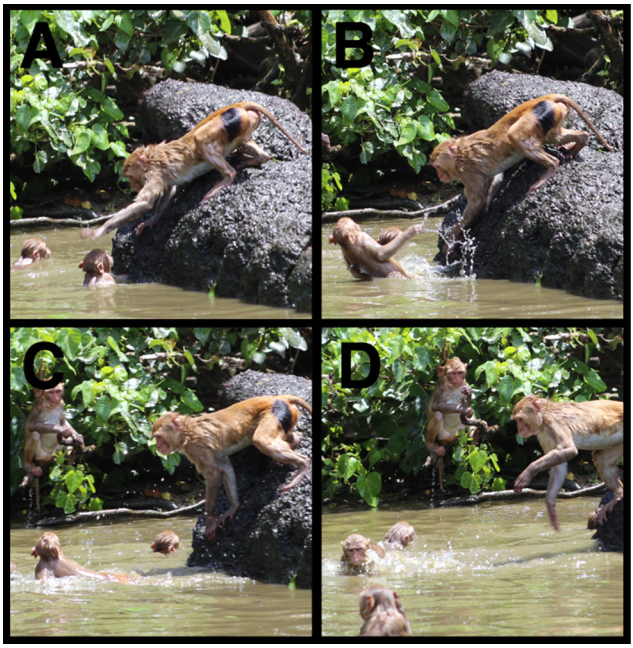

Figure 6. In addition to the diving behaviour we witnessed, many of the juveniles also engaged in play behaviour above and in the water after diving. The four panels here show a single play interaction between two juvenile rhesus monkeys, where one monkey (on the fallen log) slaps another in the water (panels A, B) before jumping into the water to chase them (panels C, D).

While we witnessed the individualistic behaviours Berman described (e.g., individuals diving from high branches, Figure 2), these occurred in the context of social interaction, often being intently observed (Figures 2 and 3, Video 10 June 2016, 04:05,00 at 10.6084/m9.figshare.13796546) and possibly mimicked by groupmates. Juveniles appeared to play associatively rather than independently (Parten, 1933) by adjusting their actions to groupmates' behaviour, especially in timing their dives (e.g., individuals rarely dove concurrently, often separated by 2–3 s (Video 10 June 2016, 04:05,00 at 10.6084/m9.figshare.13796546)). Our observations therefore suggest that aquatic play may facilitate social interaction among juvenile monkeys, presenting unique opportunities to investigate questions about possible functions of social play (e.g., cognitive development, communicative signalling practice, social network building) and the human-uniqueness of mental state representation and sharing.

Figure 7. Juvenile rhesus monkeys also engaged in affiliative play behaviour, such as cuddling, when participating in aquatic play.

4. Discussion

Previous work posits that play influences social development in many species, especially non-human primates (Vanderberg, 1978). However, little work has directly tested hypotheses about why individuals play or investigated the cognitive mechanisms that support play in non-human primates. We propose that two features of aquatic social play position it as a springboard for future research: (1) the number and diversity of participants and (2) the potential for joint experiences and shared intentions.

Given the frequency of aquatic social play and large number of individuals involved, this behaviour provides a unique platform for future work on the role of demographics and individual differences (e.g., sex, age, rank, birth order) in play likelihood. Aquatic play may offer an opportunity for more

powerful studies of individual differences than would be possible by opportunistically observing isolated instances of terrestrial social play among dyads or triads. For example, previous work proposed that play may be especially important for male macaques, who disperse at sexual maturity and must foster relationships in their new group to successfully integrate (Yanagi & Berman, 2017; Palagi, 2018). While many individuals recorded in our observations were, in fact, males, these data were collected retrospectively and opportunistically. Thus, more systematic sampling across sexes would help better characterize the role of play in social network formation (Sueur et al., 2011; Palagi, 2018; Shimada & Sueur, 2018; Mayhew et al., 2020) and successful male dispersal (Yanagi & Berman, 2017).

Similarly, future longitudinal studies of play signalling during aquatic play may provide insight into potential long-term social functions of play, including relationships with social integration, dominance hierarchies, group structure, and effective social communication (Poirier & Smith, 1974; Symons, 1974; Biben, 1998; Palagi, 2018). Previous work on play signalling in macaques found that different signals relate to different types or intensities of play (Yanagi & Berman, 2014a,b), suggesting specificity in signalling. As aquatic play includes many of these signals, like dangling and staring and looking back, as well as play behaviours like wrestling and chasing (Yanagi & Berman, 2014a), it may be helpful in identifying long-term social outcomes related to competent play signalling.

Previous longitudinal studies have often been limited to following an individual for a single developmental state (e.g., the juvenile period, from weaning to sexual maturity, ages 1–5 years). While social play provides an important snapshot into early social development, longer-term longitudinal studies could enhance our understanding of how early-life play may affect later social outcomes. For instance, identifying individuals' social aquatic and terrestrial play frequency early in life and tracking their later success in social integration could inform hypotheses about ultimate explanations of play.

Our observations may also facilitate future research into the cognitive mechanisms that support joint activities and group action in non-human primates. The social behaviour we observed closely resembles Parten's (1933) concept of associative play — as a common activity but without a clear common goal. It remains an open question to what extent non-human primates engage in Parten's concept of cooperative play — with a common goal and

distinct roles across participants (Parten, 1933). Self-handicapping behaviour provides some evidence for distinct roles (e.g., attacker vs. defender) in non-human primate play (Pellis & Pellis, 1996; Tanner & Byrne, 2010; Yanagi & Berman, 2017). However, some empirical work on forming shared goals and intentions with others, in which individuals are interdependently and simultaneously committed to achieving the same outcome, suggests this ability may be human-unique (Tomasello & Carpenter, 2007; Tomasello & Moll, 2010; Tomasello et al., 2012). Research supporting the human-uniqueness of shared intentionality shows that chimpanzees do not attempt to re-engage cooperative partners in problem solving (Warneken et al., 2006) or social games at the same rate (Warneken et al., 2006; MacLean & Hare, 2013), nor show spontaneous role reversal (Tomasello et al., 2005) as human children do. However, humans have served as non-human apes' cooperative partners in many experiments directly examining shared intentionality (e.g., Warneken et al., 2006), raising questions about whether non-human apes may behave differently with conspecifics and how these findings relate to other non-human primates (but see Heesen et al., 2020 for a recent study demonstrating re-engagement after interrupted social grooming in bonobos). The aquatic social play we observed among the rhesus monkeys on Cayo Santiago offers a new opportunity to study joint activities among non-human primates, as the behaviour appears to occur relatively frequently in this population, occurs in one fixed area, and includes many diverse participants. Therefore, future empirical work capitalizing on aquatic play may help elucidate the extent to which joint activities among non-human primates are subserved by shared goals or intentions.

Relatedly, studying links between diving and conspecific observation may inform evolutionary questions about reputation and leadership in non-human primates. In humans, risky behaviour is thought to be offset by reputation gain in some contexts (e.g., Glowacki & Wrangham, 2013). In juvenile monkeys, risk-taking (e.g., as quantified by dive height and water depth) may be motivated by reputation formation and maintenance if riskier behaviour occurs with larger audiences. An individual's initiation of group social play may also relate to later leadership of collective group actions (Strandburg-Peshkin et al., 2015, 2017) if these behaviours inform reputation.

In this brief report, we described social play in juvenile rhesus monkeys characterized by swimming and diving, in which individuals appeared to use

observations of their groupmates' actions to modulate their behaviour. However, because of the anecdotal and opportunistic nature of our observations, we recognize that there is still much to learn about aquatic play. We suggest that our observations may facilitate systematic research into both the function of social play and the cognitive underpinnings of joint activities and group action in non-human primates.

Acknowledgements

The authors share first authorship and have contributed equally. We would like to thank Evan MacLean, Laurie Santos, and Stacey Tecot for comments on an earlier manuscript, and Angelina Ruiz-Lambides, Giselle Caraballo Cruz, Bianca Giura Negru, and Nahiri Rivera Baretto for research support at the Cayo Santiago Biological Field Station, where research is supported by grants from the NIMH (R01MH096875) and the NCRR (CM-5-P40RR003640-13) to the Caribbean Primate Research Center.

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Appendix

Population information

Monkeys on the island receive no medical intervention; they are provisioned daily with Purina Monkey Chow and have ad libitum access to vegetation growing naturally on the island and collected rainwater. At one year of age, every monkey on the island is tattooed with its own unique 3-digit identification code. Monkeys are also given a combination of ear notches to aid in identification. At one year of age, paternity testing is completed such that every individual can be traced back to the colony's founding population of 400 wild-born rhesus macaques released on the island in 1939. Where possible, we identified monkeys in the photographs and videos for demographic information (see Table A3).

Table A1.
Observation information.

Observation date	Format	Location	Brief description
11 July 2015	Video	Ocean on the west side of larger island of Cayo Santiago	Juvenile monkeys seen diving and swimming in shallow coast along the west side of Cayo Santiago
15 July 2015	Video	Ocean on the west side of larger island of Cayo Santiago	Juvenile monkeys seen foraging, wrestling, chasing, and swimming in shallow coast along the west side of Cayo Santiago
10 June 2016	Video	Mangrove forest, larger island of Cayo Santiago	Juvenile monkeys seen diving one after another in collected rainwater pool
4 June 2017	Photographs	Lower corral pool, larger island of Cayo Santiago	Juvenile monkeys seen diving, playing, and observing other conspecifics in collected rainwater pool

Details from each of the observations cited in the paper, including date, observation recording format, location on Cayo Santiago, and a brief description of what occurred in the recording.

Table A2.
Definitions of play signalling and behaviour.

	Description	Image	Video
Play signal			
Dangle and stare	Subject dangles from a tree branch and stares at a conspecific[a,b]	Figure 4	15 July 2015
Gambol	High stepping walk or run in which the subject alternatively raises the front and hind legs[a,b]		15 July 2015
Play behaviour			
Chasing	Subject running, leaping, or climbing towards (attacker) or away from (defender) another conspecific without ever coming into physical contact; individuals may alternate roles[b]	Figure 6	15 July 2015
Cuddling	Two subjects mildly wrestle, holding one another in an embrace[b]	Figure 7	
Slapping	Two subjects hit each other with open-mouth play face display[b]	Figure 6	
Wrestling	Two subjects engage in mutual grasping, pushing, pulling, and rolling[b]	Figures 4, 5	
Aquatic play behaviour			
Diving	Subject jumps from a tree branch into a body of water below	Figures 2, 3	10 June 2016
Observing others	One or more conspecifics watches the subject, specifically during diving behaviour	Figures 2, 3	10 June 2016
Swimming			15 July 2015

Definitions of each of the play signals and behaviours observed in the instances of aquatic play we describe in the paper, including the figure, photo, or video, with the source of the definition cited where appropriate.

[a] Symons (1978).

[b] Yanagi & Berman (2014a).

Table A3.
Individual identification (where possible).

Figure	Action or position	Sex	Age (years; at time of photo)
Figure 2	Jumping	F	1.84
	Observing	M	2.82
Figure 3	Jumping	M	3.88
	Observing/back left	M	1.87
	Observing/right	M	1.86
Figure 4	Dangling	M	2.79
	Top/left	M	1.86
	Bottom/right	M	1.87
Figure 5	On left	F	1.84
Figure 6	Slapping	M	3.88