

State of the Field: Developmental Primate Cognition

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Abstract

A review by the *ManyPrimates* project confirmed longstanding beliefs about the field of primate cognition. Namely, research is driven by a handful of species, often from the same study site, and inferences are limited by small sample sizes. However, the review did not address another common practice in primate cognition: sampling only adults. Whereas adult data have been useful for comparisons to human literature for understanding cognitive abilities on an evolutionary timescale, these studies do not allow investigators to ask questions about the developmental processes underlying primate cognition. The purpose of this secondary systematic review was to provide a state of the field on developmental primate cognition by answering the following questions about recent publications using the *ManyPrimates* dataset: (1) how often investigators sampled infants and/or juveniles separately from adults; (2) when infants and/or juveniles were included with adults, how often was age analyzed statistically; (3) how often were studies longitudinal; (4) what topics have been studied; and (5) what techniques have been used. Results revealed that the typical recent primate cognition study did not incorporate development. Practical challenges that may preclude investigators from pursuing developmental research questions in primate cognition are discussed with recommendations to guide future research.

Keywords: developmental; primate; cognition; systematic review; *ManyPrimates*

Introduction

Cognition is broadly construed as all of the ways that animals take in and use information from their environment (Shettleworth, 2009). The term “primate cognition” refers to the body of work examining cognition in *nonhuman* primate species such as prosimians, monkeys, and apes; human comparisons may be explicit or implicit. Primate cognition as a discipline is relatively young but growing rapidly (Seed & Tomasello, 2010; see Chapter 1 this volume for a historical review). Present-day researchers in primate cognition span several different fields such as psychology, biology, anthropology, and zoology. A common thread that ties these researchers together is the challenge of sampling. Primate cognition researchers are typically limited by the species and number of individuals available in the setting where they work, whether it is in captivity or the field.

A review by the collaborative group *ManyPrimates* quantified some of the sampling biases that are well-known in primate cognition by examining recent publications from key journals (ManyPrimates, Altschul, Beran, Bohn, Caspar, et al., 2019). *ManyPrimates* reported that less than 15% of all known primate species had been studied in the five-year period from 2014-2019. The lack of species diversity was compounded by few locations publishing the majority of articles in addition to small sample sizes. Across 574 articles examined, the median sample size was 7 individuals. These sampling practices limit the conclusions that can be drawn from these studies. However, the *ManyPrimates* review did not address another common practice in primate cognition research that may be an additional source of sampling bias: the tendency to only measure adults. The traditional approach in primate cognition has answered important questions about levels of cognitive abilities in different species but has largely overlooked how these abilities develop.

The purpose of this systematic review was to reexamine the *ManyPrimates* (2019) dataset to determine if/how researchers have incorporated development in studies of primate cognition. In human cognition, developmental approaches have been widely used to understand differences in the timing and the patterning of cognitive development in various domains across infants and children using longitudinal and cross-sectional designs; however, comparable primate studies have been limited (for a review that predates the *ManyPrimates* dataset, see Rosati et al., 2014). The overall goal of this secondary analysis was to provide a state of the field on developmental primate cognition. This goal was achieved through two objectives. The primary objective was to determine the frequency with which infants and juveniles have been subjects in recent studies of primate cognition. The dataset was filtered by age class to identify the number of studies that examined infants, juveniles, or mixed age classes (i.e., adults plus infants and/or juveniles). These studies were further reviewed to determine how often a statistical analysis of age was reported, and whether the study utilized a longitudinal design in which the same individuals were assessed at two or more timepoints. The secondary objective was to summarize trends in the topics studied and the techniques used in the recent captive and field work meeting criteria for developmental primate cognition. Identifying what has been studied and what has worked from a methods perspective is important for establishing a toolkit that investigators can use to fill outstanding empirical and theoretical gaps in our knowledge of how cognitive processes develop in primates.

Methods

A secondary analysis of 574 papers published in primate cognition from 2014 to 2019 was conducted and reported using the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) guidelines (Moher et al., 2009).

Information Sources and Original Search Strategy

The original dataset was generated by the collaborative open science primate cognition group *ManyPrimates* (2019). The dataset was downloaded from a public repository available at: https://github.com/ManyPrimates/japanese_review. The search strategy in the original review was to survey the following 22 journals for work published in primate cognition between January 2014 and October 2019: *American Journal of Primatology*, *Animal Behaviour*, *Animal Behavior & Cognition*, *Animal Cognition*, *Behavioural Processes*, *Biology Letters*, *Child Development*, *Current Biology*, *Cognition*, *Developmental Psychobiology*, *Developmental Science*, *International Journal of Primatology*, *Journal of Comparative Psychology*, *JEP: Animal Learning & Cognition*, *PeerJ*, *PLOS Biology*, *PLOS ONE*, *PNAS*, *Primates*, *Proceedings of the Royal Society B*, *Psychological Science*, and *Scientific Reports*. The five inclusion criteria in the original review were articles (1) with original data; (2) from at least one nonhuman primate species; (3) that reported on a psychological process; (4) measured from at least one experimental manipulation; (5) that included behavioral data. Studies that focused on non-behavioral data were excluded. Members of the *ManyPrimates* listserv contributed additional articles that met inclusion criteria.

Study Selection and Eligibility Criteria

Only records in the *ManyPrimates* (2019) dataset were identified for screening, assessed for eligibility, and included in the secondary qualitative synthesis. The dataset was first screened for age class using an identifier provided by the original reviewers. Records that only reported on adults were excluded at this stage. A small number of records examining multiple species had more than one age class identifier in the original dataset ($n = 35$). These records were reclassified for the secondary analysis as mixed (i.e., more than one age class) and given full-text review. Full-text articles were then assessed for eligibility based on the details of age and age analyses provided in each study. Records were excluded that did not report full age details of the subjects tested; provided only adult data; did not include original data; or examined mixed age classes but did not report a statistical analysis of age. The eligibility assessment was performed by two coders evaluating each full-text record independently. Disagreements were resolved through discussion. A PRISMA flow chart for the secondary analysis performed is given in **Figure 1**.

Data Collection Process and Data Items

Data extracted from eligible studies included (1) the setting for data collection (coded as captivity or field); (2) the major topic(s) studied; (3) the major technique(s) used; (4) whether age was analyzed statistically (coded as yes or no); and (5) whether the study utilized a longitudinal design defined as two or more time points with the same subjects (coded as yes or

no). Major topics and techniques were determined from the author-provided keywords (when available) or the Methods section of the full-text. Design elements including the setting for data collection and the statistical approach were determined from the Methods and Results sections. Electronic supplements were also utilized (when available) for data collection. Data were entered into a spreadsheet by a primary coder and verified independently in a second step by a secondary coder. All authors contributed to discussion about the data collection process and final data items.

Risk of Bias

Risk of bias in this secondary analysis was mitigated by two or more of the authors reading the Methods and Results sections of each full-text article in detail during the eligibility assessment and the data collection process. Risk of bias in studies included in the original *ManyPrimates* (2019) review was not assessed, and this information was not provided by those authors.

Synthesis of Results

Eligible studies were classified into one of two results categories: (1) studies on primate cognition that examined a single age class that was not strictly adults (i.e., infants or juveniles); or (2) studies on primate cognition that examined mixed ages as defined by two or more age classes in the sample (i.e., adults plus infants and/or juveniles) with a statistical analysis of age. Only studies that sampled developmental populations separate from adults or reported an age-linked analysis with or without a longitudinal approach are discussed in the results.

Results

Study Selection

The *ManyPrimates* (2019) dataset was downloaded from the public repository, and 574 records were identified for the secondary analysis. At screening, 283 records were excluded on the basis of adult age class. The full text was obtained for the remaining 291 records, and these articles were then assessed for eligibility. Two records were excluded that were reclassified as an adult age class study upon read of the full-text, and 46 records were excluded that did not report any age details on the subjects tested. One record was excluded because it was a review paper with no original data. An additional 142 records were excluded that examined mixed age classes (adults plus infants and/or juveniles) because there was no statistical analysis of age. There were 100 articles (17% of the *ManyPrimates* dataset) included in the final qualitative synthesis (**Fig. 1**).

Study Characteristics

The included articles represent recent studies in primate cognition that did not exclusively measure adults. Articles that measured a single non-adult age class (e.g., infants only or juveniles only) are summarized in **Table 1**. Articles that measured mixed age classes (e.g., adults plus at least one infant and/or juvenile subject) and provided a statistical analysis of age are summarized in **Table 2**. In both tables, results are organized by species using the scientific name provided by the authors. Articles that reported data from multiple species are represented as one species per

row (**Table 1**, one infant article and one juvenile article; **Table 2**, 15 articles). Data from one study with two experiments that differed in age class and design is in both tables (Wobber et al., 2014). Data were collected in captivity for 79 of the articles, and in the field for 21 of the articles.

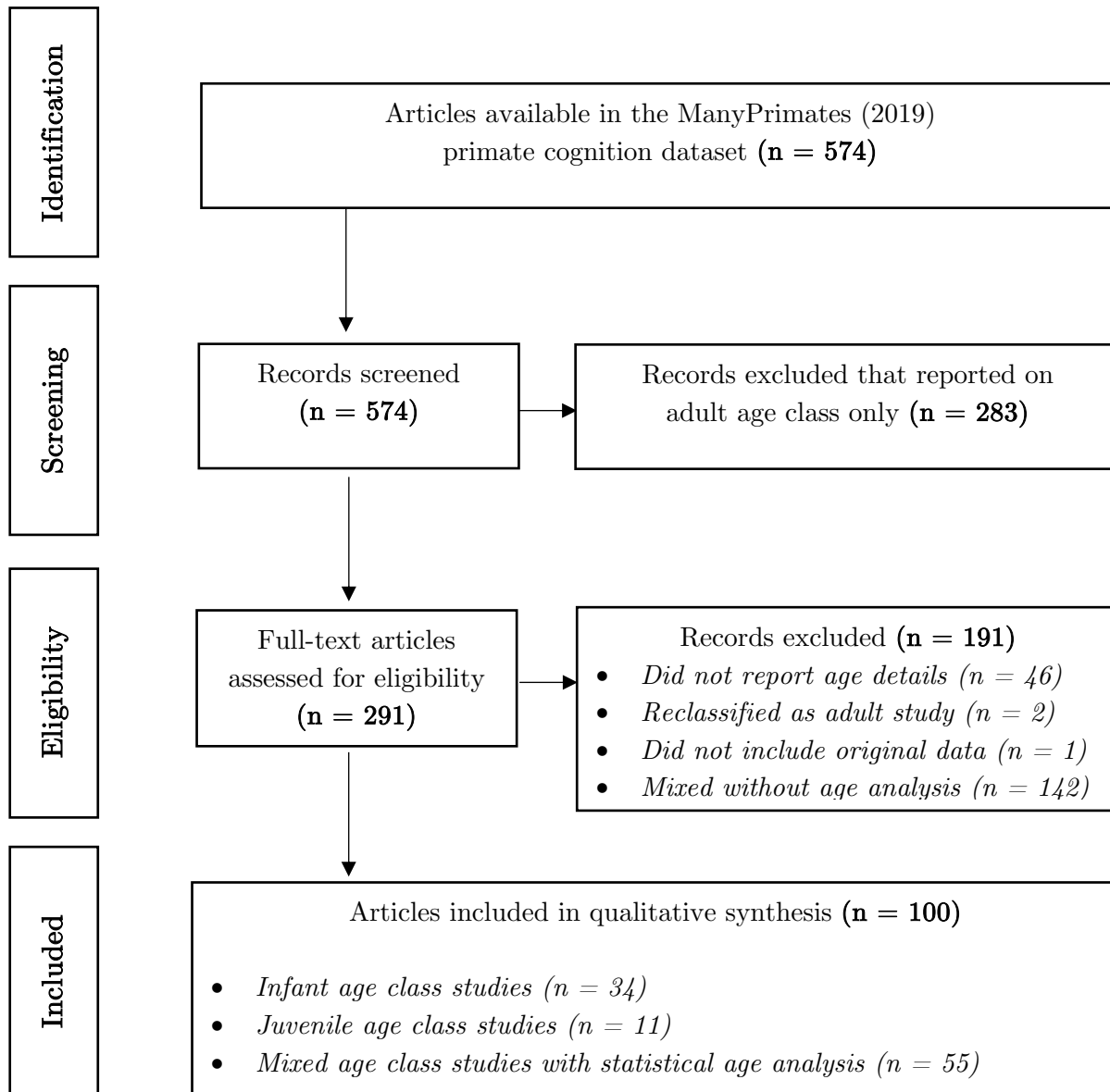


Figure 1. PRISMA flow chart.

Table 1. Infant and juvenile age class studies synthesized by species, major topic(s)/technique(s), whether a statistical age analysis was reported, and whether a longitudinal design was used. Records involving two or more species are represented as one species per row.

<i>Source</i>	<i>Species</i>	<i>Setting: Major Topic(s)/Technique(s)</i>	<i>Age Stats</i>	<i>Longitudinal</i>
Infant Age Class				
Larke et al. (2017)	<i>C. cupreus</i>	C: anxiety/open field test	Yes	Yes
Takahashi et al. (2017)	<i>C. jacchus</i>	C: vocal learning/playback study	Yes	Yes
Zhou et al. (2015)	<i>M. fascicularis</i>	C: sevoflurane exposure/observation; WGTA	Yes	Yes
Damon et al. (2017)	<i>M. mulatta</i>	C: face processing/eye-tracking	No	No
Dettmer et al. (2016)	<i>M. mulatta</i>	C: face-to-face interactions/observation; eye-tracking	Yes	Yes
Dettmer et al. (2015)	<i>M. mulatta</i>	C: cognitive testing/object detour reach task	No	No
Fawcett et al. (2014)	<i>M. mulatta</i>	C: anxiety/free play; human intruder; observation	No	No
Festante et al. (2018)	<i>M. mulatta</i>	C: mu rhythm/EEG; reaching-grasping task	Yes	Yes
Goursaud et al. (2014)	<i>M. mulatta</i>	C: attachment/observation; discrimination task; lesion	Yes	Yes
Kaburu et al. (2016)	<i>M. mulatta</i>	C: social development/neonatal imitation; observation	No	Yes
Madrid et al. (2017)	<i>M. mulatta</i>	C: face recognition/novel face preference; oxytocin biology	No	Yes
Murphy and Dettmer (2020)	<i>M. mulatta</i>	C: social experience; cognition/PNNA; cognitive testing	No	Yes
Muschinski et al. (2016)	<i>M. mulatta</i>	C: face preference/eye-tracking	Yes	Yes
Parr et al. (2016)	<i>M. mulatta</i>	C: attention/eye-tracking	Yes	Yes
Paukner et al. (2014)	<i>M. mulatta</i>	C: social attention/neonatal imitation; eye-tracking	No	Yes
Paukner et al. (2017)	<i>M. mulatta</i>	C: facial gestures; arousal/neonatal imitation	Yes	Yes
Paukner et al. (2018)	<i>M. mulatta</i>	C: social attention/observation; eye-tracking	No	Yes
Sclafani, Paukner, et al. (2015)	<i>M. mulatta</i>	C: social development/imitation	Yes	Yes
Sclafani, Simpson, et al. (2015)	<i>M. mulatta</i>	C: space perception/reaching-grasping task	Yes	Yes
Simpson, Jakobsen, et al. (2017)	<i>M. mulatta</i>	C: attention/eye-tracking	Yes	Yes
Simpson, Maylott, et al. (2019)	<i>M. mulatta</i>	C: social attention/touch task; eye-tracking	No	No
Simpson, Miller, et al. (2016)	<i>M. mulatta</i>	C: social cognition/neonatal imitation; gaze following	No	Yes
Simpson, Nicolini, et al. (2016)	<i>M. mulatta</i>	C: social motivation/human intruder; eye-tracking	No	Yes
Simpson, Paukner, et al. (2014)	<i>M. mulatta</i>	C: attention/neonatal imitation	No	No
Simpson, Sclafani, et al. (2014)	<i>M. mulatta</i>	C: social behavior/imitation tests; oxytocin administration	No	Yes
Simpson, Suomi, et al. (2016)	<i>M. mulatta</i>	C: face discrimination/eye-tracking	Yes	No
Simpson, Paukner, et al. (2019)	<i>M. mulatta</i>	C: attention/eye-tracking	Yes	Yes

(Table 1 continued)

<i>Source</i>	<i>Species</i>	<i>Setting: Topic(s)/Technique(s)</i>	<i>Age Stats</i>	<i>Longitudinal</i>
Simpson, Paukner, et al. (2017)	<i>M. mulatta</i>	C: social cognition/working memory; gaze following; oxytocin	No	No
Simpson, Sciafani, et al. (2019)	<i>M. mulatta</i>	C: social touch/memory; novelty seeking; social interest	No	Yes
Slonecker et al. (2018)	<i>M. mulatta</i>	C: infant-directed speech/habituation; eye-tracking	No	No
Vanderwert et al. (2015)	<i>M. mulatta</i>	C: facial gestures/neonatal imitation; EEG	No	No
Wooddell et al. (2019)	<i>M. mulatta</i>	C: social status/neonatal imitation; BNBAS; observation	No	Yes
Wobber et al. (2014) ^a	<i>P. paniscus</i>	C: cognitive development/CDCB	Yes	No
Wobber et al. (2014) ^a	<i>P. troglodytes</i>	C: cognitive development/CDCB	Yes	No
Bard et al. (2014)	<i>P. troglodytes</i>	C: social cognition/BSID; IBR	Yes	Yes
Juvenile Age Class				
Kawai et al. (2014)	<i>C. jacchus</i>	C: reciprocity/social exchange paradigm	No	No
Troisi et al. (2018)	<i>L. rosalia</i>	F: social learning/playback study; observation	No	Yes
Ballesta et al. (2014)	<i>M. fascicularis</i>	C: play/automatic behavioral assessment	No	No
Ballesta and Duhamel (2015)	<i>M. fascicularis</i>	C: social decision-making/primate chair; observation	No	No
Woo et al. (2018)	<i>M. fascicularis</i>	C: visual enrichment/TV; blood cortisol; observation	No	No
Ballesta and Duhamel (2015)	<i>M. mulatta</i>	C: social decision-making/primate chair; observation	No	No
Chang et al. (2015)	<i>M. mulatta</i>	C: MSR/primate chair; VST training; mark test	No	No
Monfardini et al. (2014)	<i>M. mulatta</i>	C: social learning/object discrimination task	No	No
Nelissen and Vanduffel (2017)	<i>M. mulatta</i>	C: action recognition/two-alternative categorization task	No	No
Sciafani et al. (2016)	<i>M. mulatta</i>	C: social functioning/observation; BBA; FRMT; RCSST	No	Yes
Deshpande et al. (2018)	<i>M. radiata</i>	F: intentional communication/observation; field experiment	No	No
Neves Filho et al. (2016)	<i>Sapajus</i> spp.	C: problem-solving/repertoire training; tool use task	No	No

Setting: C, Captivity; F, Field. *Topic(s)/Technique(s):* BBA, BioBehavioral Assessment. BNBAS, Brazelton Neonatal Behavioral Assessment Scale. BSID, Bayley Scales of Infant Development. CDCB, Comparative Developmental Cognitive Battery. EEG, electroencephalogram. FRMT, Face Recognition Memory Test. IBR, Infant Behavioral Record. MSR, Mirror Self-Recognition. PNNA, Primate Neonatal Neurobehavioral Assessment. RCSST, Response to Conspecific Social Stimuli Test. TV, Television. VST, Visual-Somatosensory Training. WGTA, Wisconsin General Test Apparatus.

^aInfant data are from Experiment 1. Data from Experiment 2 can be found in Table 2.

Table 2. Mixed age class studies in which a statistical age analysis was reported synthesized by species, major topic(s)/technique(s), and whether a longitudinal design was used. Records involving two or more species are represented as one species per row.

<i>Source</i>	<i>Species</i>	<i>Setting: Major Topics/Techniques</i>	<i>Longitudinal</i>
Prosimians			
Huebner and Fichtel (2015)	<i>E. rufifrons</i>	F: problem-solving; innovation/artificial feeder	No
Schnoell et al. (2014)	<i>E. rufifrons</i>	F: social learning/social diffusion experiment; artificial feeder	Yes
Reddy et al. (2015)	<i>E. macaco</i>	C: inhibition/value discrimination task; reputation-like judgement task	No
Reddy et al. (2015)	<i>E. mongon</i>	C: inhibition/value discrimination task; reputation-like judgement task	No
Kittler et al. (2018)	<i>L. catta</i>	C: problem-solving/stick task; means-end problems	No
Kulahci et al. (2018)	<i>L. catta</i>	C: problem-solving; social networks/observation; foraging task; SNA	No
Reddy et al. (2015)	<i>L. catta</i>	C: inhibition/value discrimination task; reputation-like judgement task	No
Huebner et al. (2018)	<i>M. murinus</i>	F: problem-solving; spatial learning/FE task; maze; BMI; survival	Yes
Kittler et al. (2018)	<i>M. murinus</i>	C: problem-solving/stick task; means-end problems	No
Reddy et al. (2015)	<i>P. coquereli</i>	C: inhibition/value discrimination task; reputation-like judgement task	No
Kittler et al. (2018)	<i>V. variegata</i>	C: problem-solving/stick task; means-end problems	No
Reddy et al. (2015)	<i>V. variegata</i>	C: inhibition/value discrimination task; reputation-like judgement task	No
Platyrrhines			
Amici et al. (2014)	<i>A. Geoffroyi</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Ryan et al. (2019)	<i>C. cupreus</i>	C: social cognition/eye-tracking	Yes
Taylor et al. (2014)	<i>C. Geoffroyi</i>	C: stress/social separation; hormone analysis; observation	Yes
Gunhold, Massen, et al. (2014)	<i>C. jacchus</i>	F: social learning; memory/field experiment; artificial fruit	Yes
Gunhold, Whiten, et al. (2014)	<i>C. jacchus</i>	F: social learning/field experiment; artificial fruit; video demonstration	No
Šlipogor et al. (2016)	<i>C. jacchus</i>	C: personality/GA; tNF; tNO; tP; tFUR; controls	Yes
Barrett et al. (2017)	<i>C. capucinus</i>	F: social learning/field experiment; extractive foraging task	No
Coss et al. (2019)	<i>C. capucinus</i>	F: alarm-call tonality/field recordings; harmonics-to-noise ratio analysis	Yes
Amici et al. (2014)	<i>S. apella</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Wood and Whiten (2017)	<i>S. apella</i>	C: social learning/novel problem-solving apparatus	No
Zander and Judge (2015)	<i>S. apella</i>	C: motor planning/elevated dowel task	No
Tujague et al. (2015)	<i>S. cay</i>	C: long-term spatial memory/modified radial maze	Yes
Corat et al. (2016)	<i>Sapajus</i> sp.	F: tool-use/nut-cracking task	No
Morton et al. (2016)	<i>Sapajus</i> sp.	C: social decision-making/photograph task; observation	No

(Table 2 continued)

<i>Source</i>	<i>Species</i>	<i>Setting: Major Topics/Techniques</i>	<i>Longitudinal</i>
Catarrhines			
Rivière et al. (2018)	<i>C. t. torquatus</i>	C: decision-making/gambling task	No
Botting et al. (2018)	<i>C. a. pygerythrus</i>	F: social learning/field experiment; artificial fruit	No
Isbell and Etting (2017)	<i>C. pygerythrus</i>	F: snake detection/snakeskin task	No
Darusman et al. (2014)	<i>M. fascicularis</i>	C: delayed response task performance/STMT; LTMT; MLT	No
Arnaud et al. (2017)	<i>M. fuscata</i>	F: personality/novel-object test; novel-food test; microsatellite analyses	No
Bouchet et al. (2017)	<i>M. fuscata</i>	C: vocal exchange/playback experiment	No
Bettle and Rosati (2019)	<i>M. mulatta</i>	F: theory of mind/gaze-following task	No
Gazes et al. (2019)	<i>M. mulatta</i>	C: touchscreen use/automated computerized testing; observation	Yes
Mandalaywala et al. (2017)	<i>M. mulatta</i>	F: attentional bias; stress/observation; vigilance task; saliva assay	Yes
Pfefferle et al. (2014)	<i>M. mulatta</i>	F: kin recognition/picture discrimination task; field experiment	No
Rosati et al. (2016)	<i>M. mulatta</i>	F: social cognition/gaze-following task	No
Rosati and Santos (2016)	<i>M. mulatta</i>	F: theory of mind/metacognition search task	No
Rosati and Santos (2017)	<i>M. mulatta</i>	F/C: social cognition/gaze-following task	No
Ryan et al. (2019)	<i>M. mulatta</i>	C: social cognition/eye-tracking	Yes
Molesti and Majolo (2016)	<i>M. sylvanus</i>	F: cooperation/string-pull task; observation	No
Rosati and Santos (2017)	<i>M. sylvanus</i>	F/C: social cognition/gaze-following task	No
Parron and Meguerditchian (2016)	<i>P. anubis</i>	C: gaze following/human head redirection task; habituation	No
Apes			
Amici et al. (2014)	<i>G. gorilla</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Ebel and Call (2018)	<i>G. gorilla</i>	C: problem-solving/collapsible platform tool task	No
Gustafsson et al. (2014)	<i>G. gorilla</i>	C: neophobia/novel food test	No
Palagi et al. (2019)	<i>G. gorilla</i>	C: yawn contagion/observation; avatar video task	No
Völter and Call (2014b)	<i>G. gorilla</i>	C: problem-solving/vertical maze task	No
Caspar et al. (2018)	<i>H. lar</i>	C: visual referential cues; handedness/object-choice task; tube task	No
Caspar et al. (2018)	<i>H. muelleri</i>	C: visual referential cues; handedness/object-choice task; tube task	No
Caspar et al. (2018)	<i>N. gabriellae</i>	C: visual referential cues; handedness/object-choice task; tube task	No
Caspar et al. (2018)	<i>N. leucogenys</i>	C: visual referential cues; handedness/object-choice task; tube task	No

(Table 2 Apes continued)

<i>Source</i>	<i>Species</i>	<i>Setting: Major Topics/Techniques</i>	<i>Longitudinal</i>
Caspar et al. (2018)	<i>N. siki</i>	C: visual referential cues; handedness/object-choice task; tube task	No
Amici et al. (2014)	<i>P. paniscus</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Ebel and Call (2018)	<i>P. paniscus</i>	C: problem-solving/collapsible platform tool task	No
Forss et al. (2019)	<i>P. paniscus</i>	C: neophobia/novel food test	No
Krupenye and Hare (2018)	<i>P. paniscus</i>	C: prosociality/helper-hinderer paradigm	No
Lucca et al. (2018)	<i>P. paniscus</i>	C: gaze alternation/food-requesting task	No
Tan et al. (2017)	<i>P. paniscus</i>	C: prosociality/food provisioning task; video stimuli	No
Völter and Call (2014a)	<i>P. paniscus</i>	C: tool use/multilevel trap task	No
Völter and Call (2014b)	<i>P. paniscus</i>	C: problem-solving/vertical maze task	No
Völter and Call (2018)	<i>P. paniscus</i>	C: problem-solving/mirror image experiments	No
Wobber et al. (2014) ^a	<i>P. paniscus</i>	C: cognitive development/CDCB	Yes
Amici et al. (2014)	<i>P. troglodytes</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Bohn et al. (2016)	<i>P. troglodytes</i>	C: referential communication/iconic gestures paradigm	No
Ebel and Call (2018)	<i>P. troglodytes</i>	C: problem-solving/collapsible platform tool task	No
Eckert et al. (2018)	<i>P. troglodytes</i>	C: numerical cognition/ROR experiments	No
Forss et al. (2019)	<i>P. troglodytes</i>	C: neophobia/novel food test	No
Gustafsson et al. (2014)	<i>P. troglodytes</i>	C: neophobia/novel food test	No
Henkel and Setchell (2018)	<i>P. troglodytes</i>	C: social recognition/behavioral bioassay; olfaction task; observation	No
Kret et al. (2018)	<i>P. troglodytes</i>	C: emotion processing/emotional dot-probe paradigm	No
Lucca et al. (2018)	<i>P. troglodytes</i>	C: gaze alternation/food-requesting task	No
Rosati et al. (2018)	<i>P. troglodytes</i>	C: cooperation/decision-making task battery	No
Saito et al. (2014)	<i>P. troglodytes</i>	C: representation drawing/imitation-of-model task; free drawing	No
Sirianni et al. (2018)	<i>P. troglodytes</i>	F: tool use/hammering task; camera traps; kinematics	No
Völter and Call (2014a)	<i>P. troglodytes</i>	C: tool use/multilevel trap task	No
Völter and Call (2014b)	<i>P. troglodytes</i>	C: problem-solving/vertical maze task	No
Völter and Call (2018)	<i>P. troglodytes</i>	C: problem-solving/mirror image experiments	No
Wobber et al. (2014) ^a	<i>P. troglodytes</i>	C: cognitive development/CDCB	Yes
Damerius et al. (2017)	<i>P. abelii</i>	C: problem-solving; exploration/HOI; novel food test; honey tool-task	No
Ebel and Call (2018)	<i>P. abelii</i>	C: problem-solving/collapsible platform tool task	No
Forss et al. (2016)	<i>P. abelii</i>	C: problem-solving/physical cognition tasks; novelty response tests	No

(Table 2 Apes continued)

<i>Source</i>	<i>Species</i>	<i>Setting: Major Topics/Techniques</i>	<i>Longitudinal</i>
Forss et al. (2019)	<i>P. abelii</i>	C: neophobia/novel food test	No
Gustafsson et al. (2014)	<i>P. abelii</i>	C: neophobia/novel food test	No
Völter and Call (2014b)	<i>P. abelii</i>	C: problem-solving/vertical maze task	No
Völter and Call (2014a)	<i>P. abelii</i>	C: tool use/multilevel trap task	No
Völter and Call (2018)	<i>P. abelii</i>	C: problem-solving/mirror image experiments	No
Amici et al. (2014)	<i>P. pygmaeus</i>	C: calculated reciprocity/food provisioning task; social tolerance task	No
Forss et al. (2016)	<i>P. pygmaeus</i>	C: problem-solving/physical cognition tasks; novelty response tests	No
Forss et al. (2019)	<i>P. pygmaeus</i>	C: neophobia/novel food test	No
Gustafsson et al. (2014)	<i>P. pygmaeus</i>	C: neophobia/novel food test	No
Damerius et al. (2017)	<i>P. pygmaeus</i> spp.	C: problem-solving; exploration/HOI; novel food test; honey tool-task	No
Caspar et al. (2018)	<i>S. syndactylus</i>	C: visual referential cues; handedness/object-choice task; tube task	No

Setting: C, Captivity; F, Field. *Topic(s)/Technique(s):* BMI, Body Mass Index. CDCB, Comparative Developmental Cognitive Battery. FE, Food Extraction. GA, General Activity Test. HOI, Human Orientation Index. LTMT, Long-Term Memory Test. MLT, Memory Load Test. ROR, ratio of the two ratios. SNA, Social Network Analysis. STMT, Short-Term Memory Test. tFUR, Foraging Under Risk Task. tNF, Novel Food Test. tNO, Novel Object Test. tP, Predator Test.

^aMixed age class data are from Experiment 2. Data from Experiment 1 can be found in Table 1.

Of the 100 articles in the dataset that met criteria for developmental primate cognition, 45 studies reported on a developmental sample that did not include adults (**Table 1**). Thirty-four of these studies examined cognition in infant primates across six different species: two species of platyrrhine (New World) monkeys (6%), two species of catarrhine (Old World) monkeys (88%), and two ape species (6%). However, there were no studies involving infant prosimians, and 29 of all the infant studies (85%) were on rhesus monkeys (*Macaca mulatta*). No infant study was done in the field; all of the infant articles reviewed collected their data in a captive setting. Examining the infant articles further, 14 studies (41%) included an age-linked analysis within a longitudinal design. Two additional infant studies reported a statistical age analysis but were not longitudinal (6%), and ten additional studies were longitudinal but did not examine age statistically (29%). The remaining eight articles (24%) did not analyze age statistically or utilize a longitudinal design.

There were far fewer juvenile age class articles by comparison with infant articles as seen in **Table 1**. Only 11 studies examined cognition in a juvenile sample, and these articles also spanned six different primate species: three platyrrhine monkey species (27% of juvenile articles) and three catarrhine monkey species (all macaque species, 73% of juvenile articles). No study assessed cognition in juvenile prosimians or apes. Two of the juvenile studies were field work. All other juvenile studies were done in a captive setting. No juvenile study included an age-linked analysis within a longitudinal design. Furthermore, none of the juvenile studies analyzed age statistically. One juvenile study utilized a longitudinal design, but age was not a statistical variable. Unlike the infant studies reviewed, development was almost never taken into consideration in the study design or data analysis of recent primate cognition studies involving juvenile samples.

The remaining 55 included articles reported on a mixed age class sample and included a statistical analysis of age (**Table 2**). These data represent 28% of the mixed age articles in the dataset. In other words, roughly one out of every four articles with mixed age subjects considered age in their analysis. Nevertheless, this subset of mixed age class studies included individuals from all four major primate groups. Six of the studies (11%) collectively indexed seven prosimian species, and two of these studies were longitudinal. Both longitudinal prosimian studies were field-based, and one additional study that was not longitudinal was also done in the field. All other prosimian studies examined were done in captivity. Eleven studies (20%) indexed five platyrrhine monkey species including capuchins, which are listed under different names due to controversial species-level taxonomy¹. The scientific names reported for capuchin monkeys correspond to the source article. Five of the platyrrhine studies were longitudinal. Two of the longitudinal platyrrhine studies were field-based, and three additional studies that were not longitudinal were also done in the field. All other platyrrhine studies examined were done in captivity. Fifteen studies (27%) indexed seven catarrhine monkey species. The catarrhine studies had the highest proportion of field work relative to the other taxonomic categories in **Table 2**. Nine studies (one longitudinal) were done in the field. One additional study with two data collection sites included both field and captive subjects. An additional captive catarrhine study was longitudinal, and one mixed study that was longitudinal examined both captive platyrrhine and catarrhine monkeys. Another captive study that was not longitudinal measured both platyrrhine and ape species. Finally, captive apes were the subjects of all but one of the mixed age class studies that provided

a statistical age analysis (38%). Notably, just one of 21 studies in the ape grouping was longitudinal, and it was done in captivity. Details of the major topics studied and their corresponding techniques for all included studies from **Table 1** and **Table 2** are discussed in the next section.

Results of Individual Studies

Social cognition emerged as the trending domain for studies that met inclusion criteria for this secondary systematic review of recent research in developmental primate cognition. Among the infant age class articles, major topics relating to social cognition included keywords like social attention, social behavior, social development, social motivation, social touch, and social status. Neonatal imitation was a widely used experimental paradigm, as well as eye-tracking and gaze-following to examine aspects of face processing. Behavioral observation was often used, as well as comprehensive batteries like the Brazelton Neonatal Behavioral Assessment Scale (BNBAS), the Bayley Scales of Infant Development (BSID), the Comparative Developmental Cognitive Battery (CDCB), the Primate Neonatal Neurobehavioral Assessment (PNNA), and the Wisconsin General Test Apparatus (WGTA). Several infant studies also examined the hormone oxytocin in the context of social cognition. Finally, electroencephalogram (EEG) was a technique used in exclusively in infant studies to measure electrical brain activity in conjunction with behavior.

The juvenile age class articles continued the on-trend theme of “social” in recent primate cognition publications. Related keywords included social learning, social decision-making, social functioning, and social exchange. Research with juveniles coupled behavioral observation with experimental techniques like playback study, field experiments, memory tests, and the mark test for mirror self-recognition. The use of restraint via a primate chair was unique to juvenile age class studies. On the biological level, the hormone cortisol was examined within the context of mild stress facilitating cognition. Although only one juvenile article examined problem-solving, this domain was a major theme across the mixed age class studies that included an age analysis.

Problem-solving in the included mixed age class studies was measured from performance on tool-use tasks, means-end tasks, physical cognition tasks, maze tasks, and artificial feeders. The use of artificial feeders (or artificial fruit) was also seen in captive and field studies that used social diffusion experiments to index social learning. Social inhibitory control was studied only in prosimians, whereas personality and memory were studied only in monkeys in the articles reviewed. The use of eye-tracking was also specific to monkey studies, although the broader domain of social cognition including theory of mind and gaze following tested monkeys and apes. Decision-making was studied in monkey and ape species using photographs, a gambling task, the string-pull task, and various other paradigms that indexed calculated reciprocity and prosociality. Response to novelty (i.e., food, objects) was measured in several monkey and ape studies. Nut-cracking was studied in platyrrhine monkeys and apes. Additional studies examined aspects of communication through harmonics-to-noise ratio analysis in field recordings (platyrrhine monkey study); vocal exchange through a playback experiment (catarrhine monkey study); and an experimental paradigm involving iconic gestures (ape study). Examples of topics or techniques that were specific to one species include motor planning in capuchin monkeys (*Sapajus apella*); touchscreen use in rhesus monkeys (*Macaca mulatta*), and representation drawing in chimpanzees

(*Pan troglodytes*). For additional details on the major topics and techniques of the individual studies that were included in this secondary analysis, see **Table 1** and **Table 2**. A summary of the evidence, limitations, and conclusions from this state of the field systematic review are given in the discussion that follows.

Discussion

Summary of Evidence

Results of this state of the field review revealed that the majority of recent studies (83%) in primate cognition have *not* had a developmental component as indexed by either measuring infant or juvenile samples separately from adults or including a statistical analysis of age when the research spanned multiple age classes. Of 574 articles published between 2014-2019, only 100 studies met the inclusion criteria. This number was further reduced when only longitudinal studies were considered. Just 36 studies (6% of the dataset examined) used a longitudinal design. Infant age class studies were the most likely to have employed a longitudinal design (24), followed by the mixed age class studies (11), and juvenile age class studies (1). Several sampling biases in the literature were identified including a lack of representation of prosimian species in recent infant age class research; a lack of representation of prosimian and ape species in recent juvenile age class research; an overrepresentation of rhesus monkeys across all results categories; and a disproportionate number of captive studies relative to field studies. Social cognition stood out as the leading topic among the included developmental studies and techniques leveraged different levels of analysis across this domain and other including behavior (e.g., observations, experiments), biology (e.g., cortisol, oxytocin), and the brain (e.g., EEG).

Several practical challenges may preclude investigators from pursuing research questions in developmental primate cognition. The first of these challenges is simply a lack of access to (or a sufficient number of) infant and/or juvenile primates. For example, one of the mixed age class studies that was reviewed and excluded noted an age-linked pattern in the number of trials to criterion on touchscreen-based visual object-location paired-associates learning in gray mouse lemurs (*Microcebus murinus*), and an insufficient sample size to formally test an age effect with inferential statistics (Schmidtke et al., 2018). A proposed solution to this problem of small N within individual samples is the large-scale collaborative platform *ManyPrimates*. The goal of this project is to establish a sustainable infrastructure for pooling resources in primate cognition through standardized methods facilitated by open science practices. In this collaborative framework, research topics are chosen by a vote among members and a coordination team is assembled. The topic procedure and analyses are developed prior to data collection, and pre-registered. Participating institutions implement the standardized methods with multiple checks to ensure consistency across sites, and data are uploaded to a central location for analysis and writing. Large datasets can be generated that are beyond the capabilities of any individual researcher or site. A pilot study of short-term memory that included individuals in mixed age classes and a statistical analysis of age has demonstrated feasibility for *ManyPrimates* (ManyPrimates, Altschul, Beran, Bohn, Call, et al., 2019). The *ManyPrimates* pilot included participating sites

with infants or juveniles in the social group as well as details regarding the facility's breeding plan. As more collaborators join the *ManyPrimates* project, there may be opportunities to design studies to specifically address development in the topics chosen for investigation. One step towards that goal would be to encourage data collection across age classes, and particularly solicit infant and juvenile samples. Currently researchers do not indicate the ages of potential subjects when they register interest in participating in data collection for *ManyPrimates*. Any site that meets the ethical guidelines can contribute data. Although there has been a call for contributions from researchers with access to understudied species, there has been no effort yet to sample understudied ages.

A second challenge for developmental primate cognition is that when younger animals are available in the sample that a researcher has access to, they do not participate in cognitive testing. Many cognitive paradigms test animals singly. However, infants are not routinely separated from mothers because of the distress it may cause both individuals. Many of the infant studies included in this state of the field review tested nursery-reared monkeys, rather than their mother-reared counterparts. A noted exception is the study by Dettmer et al. (2015) that developed a cognitive testing apparatus for socially housed mother-reared infant monkeys. The apparatus consisted of a tunnel between the main cage and a testing cage that was sized to only allow the infant to pass through. While in the test cage, the infant remained in visual and tactile contact with its mother and could also freely move back and forth for contact comfort. In the test cage, the infant was free to interact with a cognitive testing board as much or as little as it wanted with no interference from its mother or another adult. The entire social group was acclimated to the new apparatus before the study began until infants entered the testing cage freely to obtain a reward. Infants were easily trained and tested on the object detour reach task with this innovative setup, and the research team was able to demonstrate feasibility for testing mother-reared monkeys as young as 4-months-old on cognitive tasks for the first time – an important milestone in primate cognition. In a follow-up study that utilized the same testing setup for socially housed mother-reared infants, Murphy and Dettmer (2020) demonstrated that it is possible to directly compare mother-reared and nursery-reared monkeys on the same tasks indexing reward association, cognitive flexibility, and impulsivity. One implication from this work is that modifying the testing environment, when it is possible to do so, may facilitate infants' participation in developmental cognition research. If the testing environment cannot be modified (such as in a zoo or sanctuary setting), distracting non-focal subjects may allow individuals that would otherwise not participate in research to be tested. This recommendation is in line with guidance from *ManyPrimates* about testing in social groups.

Additional advances in methodologies will also increase participation across age classes in primate cognition testing and can easily be used in longitudinal designs. For example, Gazes et al. (2019) utilized automated touchscreen computer stations together with RFID microchip identification to track participation in cognitive testing longitudinally in a large naturalistic group of juvenile and adult rhesus monkeys. Providing multiple testing stations that are open throughout the day reduces competition and can increase participation in juvenile or low-ranking animals. In another example, Ryan et al. (2019) developed a noninvasive eye-tracking method that eliminates the need for restraint or sedation that has typically been needed to collect these data in primates.

The new procedure involves a modified transport box that can be used not only with monkeys of different species and sizes, but different ages including infants. Together these studies suggest a growing interest in ecological approaches for primate cognition (for a review and additional recommendations on measuring primate cognition in social settings, see Cronin et al., 2017). A strength of *ManyPrimates* is that their shared procedures do not require expensive apparatuses. However, sites with existing technology like touchscreens or eye-trackers could collaborate on a smaller scale to enhance rigor and reproducibility in developmental primate cognition.

A third challenge in developmental primate cognition is that longitudinal studies by their nature require repeated assessments. However, when the same individuals have been tested in different studies, concerns have been raised that their performance may be tied to familiarity with cognitive testing and not to the cognitive ability itself (e.g., ManyPrimates, Altschul, Beran, Bohn, Caspar, et al., 2019). As a counterpoint to this claim, participation history in prior research is never reported in comparable cognitive studies in humans. In fact, it is a common practice in research involving human children to contact families who have participated in a previous study when their child is eligible for a new study. Rather than a limitation, the ability to retest individuals and track their performance over time coupled with longer lifespans is a largely untapped strength within primate cognition as compared to other animal models, or developmental research with humans. Longitudinal studies require a greater investment of time and resources than cross-sectional or single timepoint designs. Sharing data collected on the same individuals would permit analyses of the relations within and between cognitive domains, as well as at key periods over the lifespan. Secondary developmental analyses may be possible with long-term success of *ManyPrimates*.

Limitations

The purpose of this secondary review was to provide a state of the field on developmental primate cognition by answering the following questions on recent publications: (1) how often investigators sampled infants and/or juveniles separately from adults; (2) when infants and/or juveniles were included with adults, how often was age analyzed statistically; (3) how often were studies longitudinal; (4) what topics have been studied; and (5) what techniques have been used. A limitation of this approach was that studies falling outside of the 5-year range were not included. There is older literature in the gaps identified including studies involving infant prosimians (e.g., Chapman et al., 2010) and longitudinal studies involving juvenile apes in captivity (e.g., Bjorklund et al., 2000) and in the field (Biro et al., 2003). In addition to these influential studies and others, newer studies that would fit the review criteria have been published, including several field studies that fill gaps identified in this review. Truppa et al. (2021) examined age-related differences in motor planning in infant, juvenile, and adult wild capuchins and Bründl et al. (2021) documented developmental milestones in motor, communication, and social skills in wild infant chimpanzees. These studies are important to note because they show feasibility for successfully implementing an experimental task in a field setting, as well as collecting longitudinal observations in the field. In another example of a recently published field experiment, Arre et al. (2020) reported on the development of theory of mind in a large sample of infant and juvenile rhesus monkeys using a looking-time task that had been validated previously in adult rhesus monkeys and human infants.

Age class differences were observed, although the study was not longitudinal. Critically, the authors drew attention to the paucity of mixed age class studies across the lifespan on their topic. Another limitation of this review is that it focused on early development and did not address cognitive change in older individuals (for recent work on age-related decline in primate cognition, see Hopkins et al., 2020; Lacreuse et al., 2020). Finally, this review focused on what kinds of developmental data have been collected and the ways those data have been analyzed. Interpreting the findings of the included articles was outside the scope. Historical reviews that are centered on a specific topic or a set of related topics, or focused comparative reviews that include human data, would provide a more complete understanding of the knowledge gaps in the many domains that are studied in developmental primate cognition.

Conclusions

Although developmental studies are not the norm in primate cognition, the articles examined in this state of the field review demonstrate feasibility for developmental approaches across topics, tasks, species and settings. Taken together, this secondary analysis extends the call from *ManyPrimates* for large-scale collaboration to pool resources in order to be able to rigorously test questions regarding how cognitive processes develop in primates. Minimally, data collection in future primate cognition research should include mixed age classes rather than a single age class. Ideally, study analyses should include a longitudinal component to track change over time in the same individuals. Effort is needed to increase involvement of field primatologists in data collection for *ManyPrimates*. Moving away as a field from testing only adults to examining the developmental context for cognition will provide a richer window into the minds of primates.

Footnotes

¹For a detailed discussion of capuchin taxonomy, see Lynch Alfaro et al. (2012).

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