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Primate Enrichment Categories: A Literature Review of Current Trends

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Abstract – Environmental enrichment aims to enhance primate wellbeing by providing physical and mental stimuli to address the biological and psychological needs of individuals. However, lack of knowledge regarding the development of enrichment research hampers implementors and future inquiries. Therefore, a collection of data from 227 peer-reviewed and freely available articles on primate enrichment (published from 1978 to 2019) was performed to present enrichment trends and outcomes through descriptive statistics. Behavior was the most recorded parameter (*n*=203), whereas physiological data were reported less frequently (*n*=20). Feeding enrichment (*n*=87) and tactile enrichment *(n*=62) were the most investigated enrichment categories, while other categories, such as olfactory enrichment (*n*=5) gained less attention. A total of 71 primate species were recorded across zoological (*n*=57), laboratory (*n*=22), and unspecified (not stated) research settings (*n*=5), with laboratory environments being predominant (*n*=135) over zoological environments (*n*=87). Notably, a substantial majority of published articles (>99%) achieved their initial research rationale, which represents a potential publication bias. To advance our understanding of enrichment welfare benefits and the specific relevance of individual enrichment methods to different primate species and taxa, a comprehensive meta-analysis incorporating all peer-reviewed primate enrichment research is crucial. Subsequent primate enrichment studies should prioritize the investigation of underrepresented enrichment categories, species, and environmental conditions, thus fostering a more comprehensive understanding of how environmental enrichment impacts primate welfare.

Keywords – Environment enrichment, Descriptive statistics, Primate welfare, Laboratory, Zoo

Non-human primates (henceforth primates) are housed in captivity for their biomedical, conservational, educational, and research value (Tardif et al., 2013; Tribe & Booth, 2003). Captive conditions can elicit a range of stress responses due to various persistent abiotic factors (e.g., artificial lighting), and biotic factors (e.g., visitor presence), or the lack of environmental complexity, all which can compromise welfare (Morgan & Tromborg, 2007). To achieve optimal welfare for primates, environmental enrichment (henceforth EE) is employed to promote behavioral complexity and alleviate captivity associated stress (Lutz & Novak, 2005; Mellen & MacPhee, 2001).

The recognition of the significance of EE began with Yerkes (1925) and was further advanced by Hediger (1950, 1969), who pioneered the promotion of captive animal welfare as a discipline. EE has evolved over-time and has been implemented in both laboratory and zoological settings (Buchanan-Smith, 2010; Fernandez & Martin, 2021; Mellen & MacPhee, 2001). However, no universal definition of EE has been accepted as an industry standard (Fernandez, 2022; Hoy et al., 2010; Mellen & MacPhee, 2001; Shepherdson, 2003). For the purposes of this review, I will used a definition of EE based on a combination of definitions provided by Fernandez (2022) and Lyn et al. (2020), which follows as “any alteration, stimuli, or procedure that is added to or modifies an animal's ex-situ environment, with the intent to improve the animal's biological, physiological, or psychological welfare (i.e., wellbeing or wellness)". Broadly, EE can be categorized as: cognitive, feeding, sensory (auditory, olfactory, and visual), social, structural, tactile, and training (Maple & Perdue, 2013).

Traditionally, EE has aimed to enhance animal welfare in captivity by promoting species typical behavior (e.g., play and foraging) and reducing undesirable behaviors (e.g., self-mutilation and other stereotypies) (Markowitz, 1979; Moberg, 2000; Shyne, 2006). The definition of animal welfare has depended on each individual's perspective, resulting in multiple definitions being used historically (Fraser, 2008). For example, Broom (1986) defined animal welfare as "the state of an individual in terms of its efforts to cope with its environment" (p. 524). More recently, Fraser (2009) emphasized comprehensive evaluation of animal welfare, through considering together the animal's physical health, functioning, affective states (e.g., distress, pain), and the opportunity to express natural behavior throughout their life.

Modern enrichment techniques aim to consistently promote high standards of animal welfare by addressing the biological and psychological needs of individuals through factors, such as diet, environmental complexity, species-specific behaviors, physical activity, environmental control, and psychological well-being (Boere, 2001; Buchanan-Smith, 2010; Newberry, 1995; Shepherdson, 2003). However, the study of EE results in challenges in understanding the intricate and individualized responses of animals to enrichment. Factors such as species, predisposition, habituation rate, previous life experiences, and enclosure complexity can intersect and influence the impact of EE on the user (Freeman & Gosling, 2010; Mellen & MacPhee, 2001; O'Neill et al., 1991; Ross et al., 2009). Consequentially, EE research has expanded to include a range of welfare measurements (e.g., biochemical stress markers, animal emotional states, and effects on neurology), while also expanding into the fields of wildlife conservation and veterinary medicine (Boissy et al., 2007; de Azevedo et al., 2007; Hüttenrauch et al., 2016; Liu et al., 2006; Sanders & Fernandez, 2020).

EE is one of the most studied aspects of captive animal welfare, with this research mostly focusing on mammals, predominantly primates (Alligood and Leighty, 2015; Binding et al., 2020; Riley & Rose, 2020). When providing EE to primates, it is important both to consider the species and individual traits of the animal to allow for in individualized management plans (Coleman, 2012; Norman et al., 2021). However, there is currently a lack of analysis regarding the progress of primate EE at the species level, across enrichment categories, and in various captive settings. Given that a key aim of EE is to meet species' natural history, then consideration of enrichment design and implementation at the species level is key for progress to be made (Mellen & MacPhee, 2001). Accordingly, in this review I aim to: 1) generate descriptive statistics on research trends and outcomes for research evaluating EE; 2) analyze primates' welfare outcomes following the provision of EE; 3) identify knowledge gaps; 4) establish a foundation for a meta-analysis; and 5) provide guidance for future research.

Methods

Literature Search

In December 2019, I used 'Google Scholar' (https://scholar.google.com) to conduct an extensive search of the peer-reviewed literature on EE. Articles that I identified but were either behind a paywall or otherwise inaccessible were requested through direct communication with the authors or alternative websites, such as Research Gate (https://researchgate.net). The search results were not restricted by the publication year, and the Boolean phrase 'AND' was used to separate each phrase in 'term 1' and 'term 2' (Table 1). Search terms were unrestricted and could be reflected in the article titles, abstracts, or key phrases. I concluded the literature search when no new relevant articles were found on the tenth search page. If I found relevant articles on the tenth page (see Inclusion Criteria), I continued the search until two consecutive pages of non-relevant results were encountered (see Exclusion Criteria) (Figure 1).

Table 1

List of Search Terms

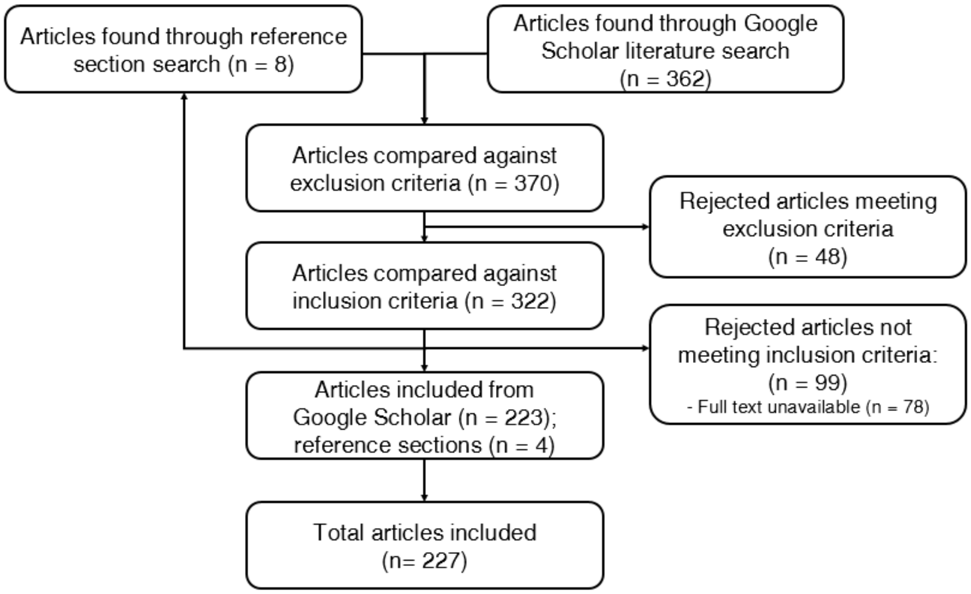
Term 1	Term 2	
Auditory Enrichment	Ape	Mangabey
Cognitive Enrichment	Aye-aye	Marmoset
Enclosure Enrichment	Baboon	Monkey
Environmental Enrichment	Bonobo	Muriqui
Feeding Enrichment	Capuchin	New world monkey
Food Enrichment	Chimpanzee	Old world monkey
Olfactory Enrichment	Colobus	Orangutan
Physical Enrichment	Drill	Potto
Social Enrichment	Galago	Prosimian
Structural Enrichment	Gelada	Primate
Tactile Enrichment	Gibbon	Sakis
Training Enrichment	Gorilla	Siamang
Visual Enrichment	Kipunji	Sifaka
	Langur	Simian
	Lemur	Talapoin
	Loris	Tamarin
	Macaque	Tarsier
	Mandrill	Titi
		Uakari

Note. The Boolean phrase AND was used, between each word of Term 1 and Term 2, e.g., Visual enrichment AND Ape.

I also searched the reference sections of all included articles for the terms listed in Table 1. This step aimed to identify additional articles that may have been missed by the Google Scholar search algorithm. The reference search process was iterative, including articles obtained from previous searches. This iterative approach ensured that all available articles were included. I repeated this process until no new articles met the inclusion-exclusion criteria outlined in Figure 1.

Figure 1

Flowchart of Inclusion and Exclusion Process



Note. Number of papers placed through the inclusion and exclusion protocol are represented in brackets. Hyphened text represents a subsection of the sections total data.

Articles that met all following inclusion criteria were included for analysis: 1) published in a peer-reviewed academic journal; 2) a full text of the article could be freely obtained and the article was written in English; 3) the article stated anywhere in the text that EE was tested, or a method, or stimulus that is enriching or enhancing to an animals welfare or wellbeing was measured, or the author(s) state a previously unknown element is enriching; and 4) the studies involved at least one primate species studied within an ex-situ enclosure.

Exclusion Criteria

Articles were excluded from this review if they met any of the following criteria: 1) they did not meet the inclusion criteria, such as being unavailable in full-text due to institutional restrictions and not accessible from alternative sources; and 2) negative stimuli removal during the experimentation period (e.g., removal of aggressive cage-mate), due to conflation with EE effects.

Recorded Characteristics

I recorded the following information from each article: 1) genus; 2) species; 3) journal name; 4) article publication year; 5) research aims; 6) primates facility category (zoological, laboratory, not stated); 7) behavior recorded (yes / no); 8) if yes, recording method used; 9) physiological data recorded (yes / no); 10) if yes, recording method used; 11) all EE categories (auditory, cognitive, feeding, olfactory, social, structural, tactile, training, and visual); 12) did author(s) combine EE category results into a single result (yes / no); 13) did the author(s) state their enrichment to have a beneficial effect upon their primate(s) (yes / no / not stated); and 14) did the author(s) consider their enrichment to produce a detrimental effect upon their primate(s) (yes / no / not stated).

I categorized primates as studied in three ex-situ settings (zoological, laboratory, and not stated), due to setting specific stimuli (e.g., repetitive stranger presence in zoos, and medical testing in laboratories). The zoological category includes establishments whose goal is primarily conservation and public education such as zoos, wildlife sanctuaries, and safari parks. The laboratory category includes establishments whose goal is primarily scientific research, including scientific laboratories, university laboratories, and breeding centers.

Descriptive Statistics

I collected enrichment characteristics data, including count and binomial data (see Recorded characteristics), and organized them based on the year of publication. This analysis aimed to assess the progression of freely available primate EE research over time and provide insights for future studies. These data were selected due to their accessibility and ease of integration, enabling a comprehensive understanding of the abundance and trends in the field. The methodology, results, discussion, and supplementary materials sections of each included article were thoroughly examined to obtain these data.

Bias Reduction

To reduce inclusion bias, I required that the topic of EE was identified explicitly by the articles author(s), rather than from inferences drawn about the topic during the literature review. This limited the range of included articles to after the 1950's when EE (or the synonym environmental enhancement) became adopted scientific parlance. Accordingly, no publications before 1978 were included because they did not pass the inclusion-exclusion protocol (n=6), or they were inaccessible (n=1).

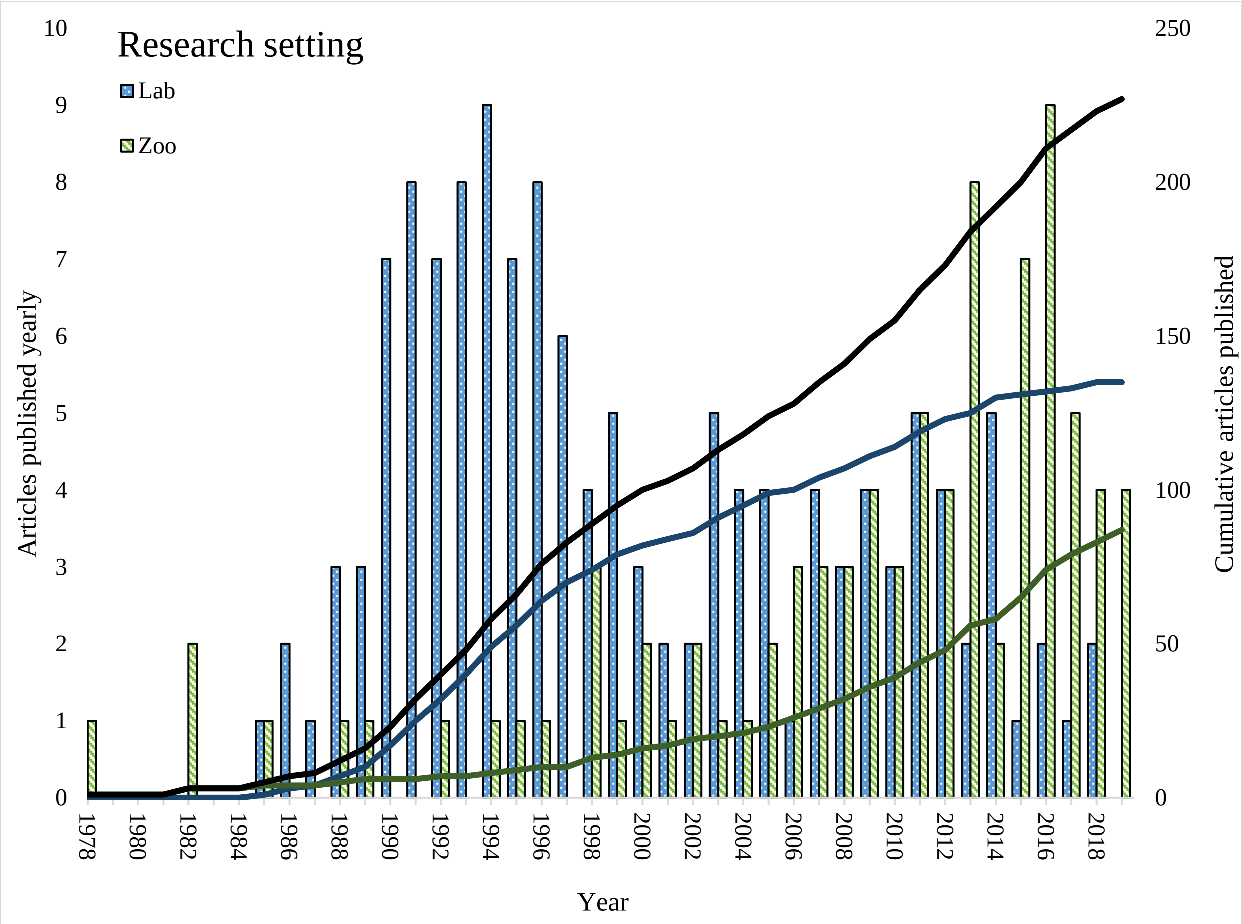
Furthermore, I reduced bias in recording EE outcome, by placing EE outcome determination upon the articles author(s). A beneficial or detrimental welfare result was recorded if the author(s) stated that the enrichment had either effect (or synonym) on the primate. If the author(s) stated that the enrichment had no beneficial or detrimental effect, then this was recorded as 'none' under their respective effect column. A single EE publication could produce multiple results, depending on the number of EE categories tested and their respective outcomes.

Results

Ultimately, 227 articles were included in this review, representing publications from 1978 to 2019. The articles were published in 48 peer-reviewed journals. The annual publication rate of primate EE articles remained relatively stable (mean=5.4; range=11) over the 42-year period (Figure 2). Laboratory-based enrichment papers (n=135) were published more than zoological-based papers (n=87). However, starting from 2008, the number of primate EE publications in zoological settings has either matched or exceeded those in laboratory-based settings (Figure 2).

Figure 2

Yearly and Cumulative Publication of Peer-Reviewed Primate Environmental Enrichment Papers Between Research Settings

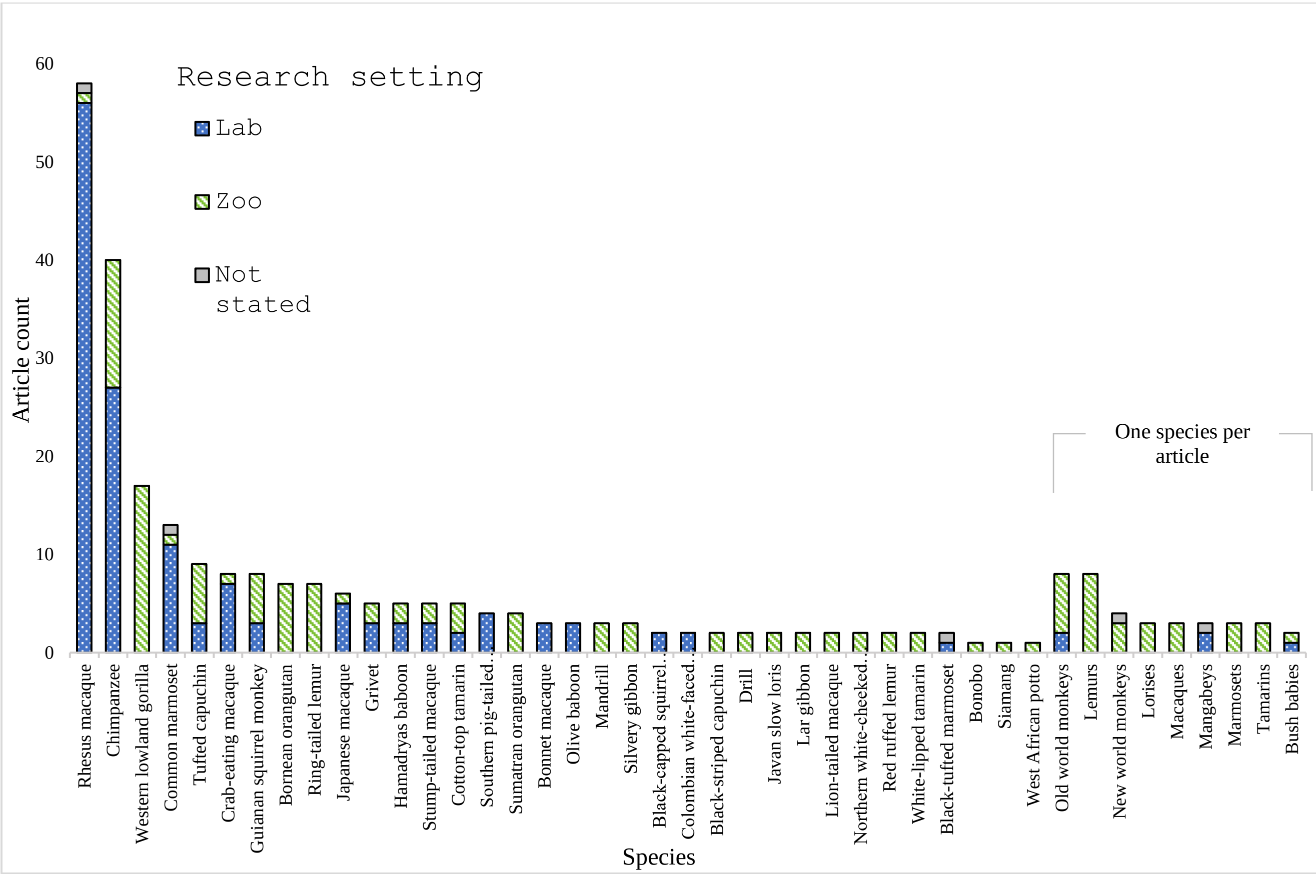


Note. Yearly article output on the primary (left) Y axis (laboratory = spotted blue bar, and zoological = stripped green bar). Cumulative article output on the secondary (right) Y axis (laboratory = dark blue line, zoological = dark green line, and total article amount = black line). "Not stated" research settings excluded.

The EE articles featured 71 species (Table S1), with rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*) being the most studied species. Research conducted in zoological settings included more primate species (n = 57) than laboratory settings (n = 22), with 11 species represented within both settings. The research setting could not be determined in four articles, resulting in five species being placed into the "not stated" category (Figure 3).

Figure 3

Research Setting and Species Representation within Primate Environmental Enrichment Papers



Note. Species represented within each research setting; laboratory (blue dotted bars), zoological (green stripped bars), and not stated (solid grey bars). The primate groups section represents an amalgamation of species present only once each in the literature. For a list of all species see Table S1.

Article Research Rational

Most articles aimed to investigate the effect of enrichment on behavior (42%) or welfare/wellbeing (12%) while, many articles explored multiple rationales (Table 2). Among the 227 articles analyzed, only one stated their initial hypothesis was not achieved. Specifically, Gentry and Margulis (2008) reported increased aggression and an unstable mixed-species group dynamics instead of an enriching and stable group dynamic.

Recording Measures

Of the 227 included articles 89% recorded primate behavior using various methods (Table 3), while 55% also used other sampling methods (e.g., social proximity) (Table 4).

Physiological data were recorded alongside behavioral data in 16 articles, while physiological data was the sole measurement in four articles. Measuring cortisol levels was the most used physiological welfare indicator (44%), however other methods were also used (Table 5)

Table 2

Enrichment Article Research Rationales Divide Between Research Organization

Aims	Total	Lab	Zoo	Not stated
Investigate enrichment effect on behavior	118	66	49	3
Investigate enrichment effect on welfare / wellbeing	34	9	25	0
Test device / method as enrichment	21	17	4	0
Reduce stereotypical / abnormal / stress related behavior	21	14	7	0
Investigate effects on social group / social behavior	14	8	6	0
Investigate foraging behavior	11	8	3	0
Explore effects on activity budget	10	4	6	0
Effects on aggression	8	3	5	0
Evaluate enrichment preference	7	6	1	0
Investigate enrichment temporal use	7	7	0	0
Enrich environment	6	4	2	0
Investigate enclosure use	4	2	2	0
Develop enrichment assessment method	3	2	1	0
Document diet preference	2	1	2	0
Increase food acceptance rates	2	1	1	0
Investigate enrichment effect on cortisol	2	2	0	0
Investigate effects on body weight	2	2	0	0
Investigate effect of enrichment on injury recovery time	2	2	0	0
Modify culture	1	1	0	0
Work for reward	1	1	0	0
Cognitive ability testing	1	1	0	0
Elicit tool use	1	1	0	0
Enrichment safety test	1	0	0	1
Enrichment durability testing	1	1	0	0
Demonstrate training method	1	1	0	0
Effect on cell-mediated immune responses	1	1	0	0
Organization Total	282	165	114	4

Note. Several articles included more than one rationale. Therefore, the number of rationales is greater than the sample of articles (n = 277).

Table 3

Number of Behavioral Observation Methods Recorded

Behavior Record Method	Total Amount	Lab	Zoo	Not stated
Interval sampling	110	60	48	2
Focal sampling	77	47	29	1
Scan sampling	59	23	35	1
Continuous sampling	56	34	21	1
Instantaneous sampling	35	12	23	0
Frequency count	20	16	4	0
All-occurrence sampling	19	7	11	1
One-Zero method	11	6	5	0
Ad libitum	6	1	4	1
Function of occurrence	1	0	1	0

Note. Several articles included more than one recording method. Therefore, the number of methods recorded is greater than the sample of papers (n = 277).

Table 4

Other Sampling Methods Split Between Research Organization

Other Sampling Methods	Lab	Zoo	Not stated
Behavioral diversity index	1	1	0
Birth interval	0	1	0
Calorie count	1	0	0
Capture time	1	0	0
Distance travelled	0	1	0
Enrichment acceptance rate	1	0	0
Enrichment activity over time	4	2	0
Enrichment competitiveness score	0	1	0
Enrichment contact over time	5	0	0
Enrichment habituation rate	3	4	0
Enrichment labor cost	1	0	0
Enrichment latency	2	1	0
Enrichment monetary cost	4	0	0
Enrichment preference	8	4	0
Enrichment proximity	1	2	0
Enrichment task selection	1	0	0
Enrichment trials completed	6	0	0
Emotional state	1	0	0
Enclosure location	27	22	1
Enrichment resilience	3	1	0
Food consumption / removal rate	8	2	0
Group cohesion rating	0	1	0
Hair loss	1	0	0
Health check	6	0	0
Infant development	1	0	0
Injury recovery period	2	0	0
Nutrition	2	0	0
Questionnaire	0	3	0
Rank relationship	5	1	0
Social proximity	12	10	1
Work for enrichment access	1	0	0
Wounding rate	2	1	1

Note. Excludes specific behavior and physiological measurement methods.

Table 5

Physiological measures used to quantify environmental enrichment effects.

Physiological Measure Method	Total	Lab	Zoo	Not stated
Cortisol	8	6	2	0
-Blood / Plasma	*4*	*3*	*0*	*0*
-Fecal	*3*	*1*	*2*	*0*
-Saliva	*1*	*1*	*0*	*0*
-Urine	*1*	*1*	*0*	*0*
Body weight	4	4	0	0
Heart rate	2	2	0	0
Blood Pressure	1	1	0	0
Whole blood serotonin	1	1	0	0
Immune response	1	1	0	0
Cortical mapping	1	1	0	0

Note. Cortisol is split between Blood/Plasma, Fecal, Saliva, and Urine. Several articles included more than one measure method. Therefore, the number of methods used is greater than the sample of papers using physiological measures (n = 18).

Enrichment Categories Outcomes

Of the 227 articles analyzed, a total of 358 EE types were tested, and in nearly 64% of the publications, the results of different enrichment categories were combined into a single mixed outcome, preventing the determination of the individual effects of each stimulus when appropriate (e.g., when separate tactile and feeding enrichments are given simultaneously) (Table 6). Feeding enrichment was the most published category, while olfactory enrichment was the least. The vast majority of cognitive, structural, and visual EE research has been undertaken in laboratories, whereas the other forms of EE have been studied more evenly across zoos and laboratories, except olfactory enrichment which has solely been studied in zoos (Table 6). A notable disparity is observed in species representation, with Lowland gorilla (*Gorilla gorilla gorilla*), chimpanzee, and rhesus macaque being the most studied in all respective enrichment categories, with fewer discrepancies in the least published categories (Figure 4), and greater disparities in the most published categories (Figure 5).

Table 6

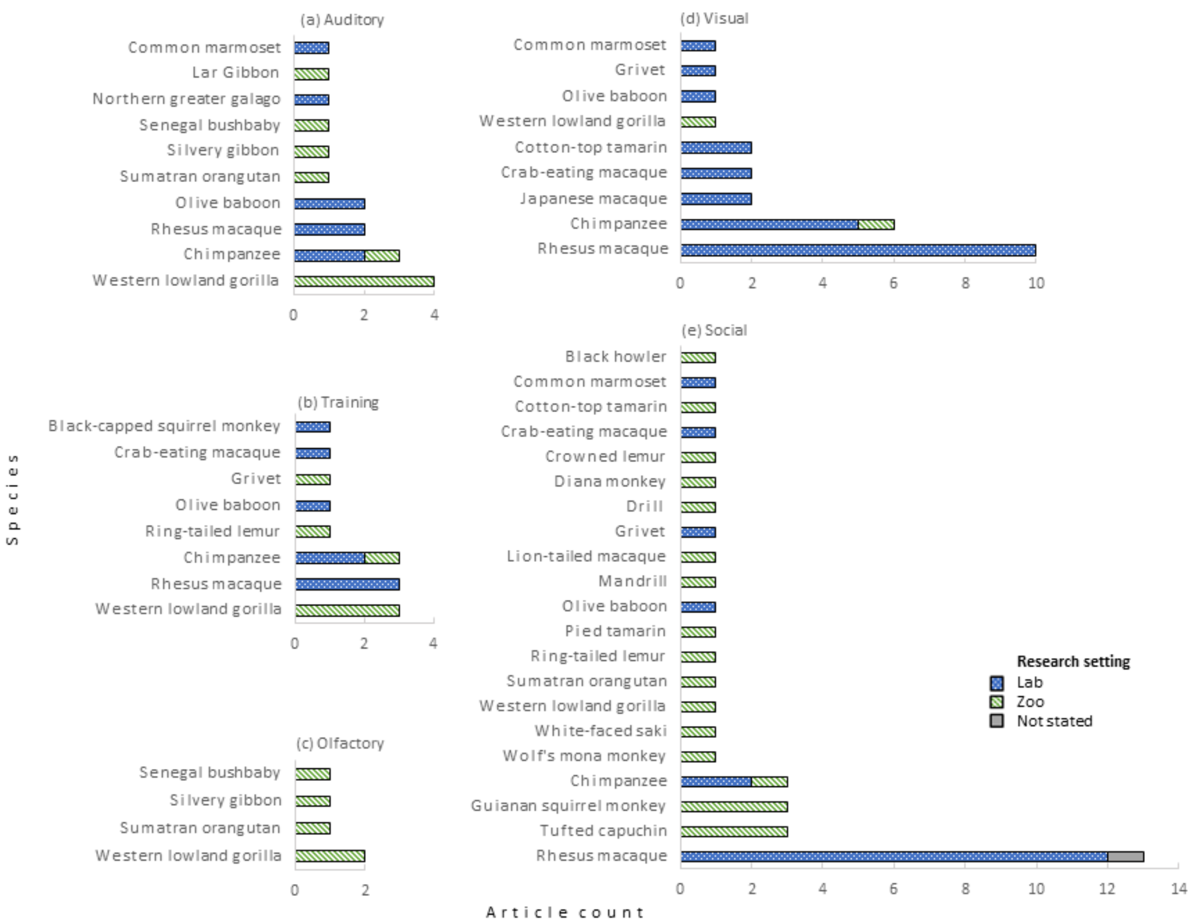
Environmental Enrichment Category Characteristics

		Enrichment Category								
		Auditory	Cognitive	Feeding	Olfactory	Social	Structural	Tactile	Training	Visual
Total articles		17	52	87	5	28	68	62	14	25
Mean article output per year		0.4	1.2	2.07	0.11	0.66	1.61	1.47	0.33	0.59
Number of articles combining enrichment category results		4	20	56	4	13	37	48	4	14
Number of articles not combining enrichment category results		13	32	31	1	15	31	14	10	11
Number of species studied		10	18	50	4	21	27	28	8	9
Enrichment setting %	Laboratory	47	71	46	0	61	72	68	57	92
	Zoological	53	29	52	100	36	25	31	43	8
	Not stated	0	0	2	0	3	3	1	0	0

Note. Individual enrichment category outcomes could not be determined from articles which combined their enrichment into a single result.

Figure 4

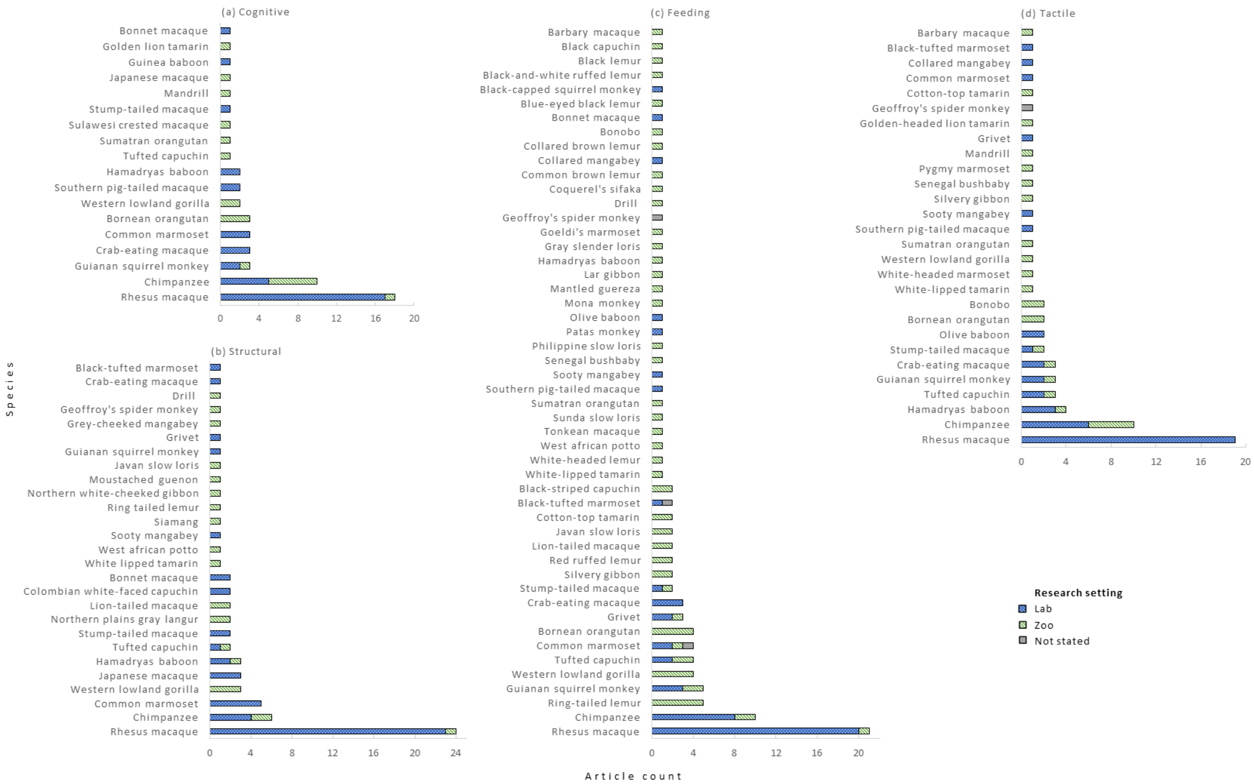
Species Representation in the Least Published Enrichment Categories



Note. Species represented within each research setting; laboratory (blue dotted bars), zoological (green stripped bars), and not stated (solid grey bars). Several articles included more than one species.

Figure 5

Species representation in the most published enrichment categories.



Note. Species represented within each research setting; laboratory (blue dotted bars), zoological (green stripped bars), and not stated (solid grey bars). Several articles included more than one species.

Overall, the results recorded more beneficial outcomes (e.g., reduced self-mutilation), than a lack of beneficial outcomes or detrimental outcomes. Furthermore, fewer detrimental outcomes (e.g., increased stereotypies), are recorded than a lack of detrimental outcomes, and articles reported more not detrimental outcomes than not beneficial outcomes. These patterns are consistent across EE category, whether single enrichment categories were utilized or when articles combined enrichment category results (Table 7).

Table 7

Article and Environmental Enrichment Category Welfare Outcomes

	Outcome	Enrichment Category									Article		
		Auditory	Cognitive	Feeding	Olfactory	Social	Structural	Tactile	Training	Visual	Single enrichment category	Combined enrichment category	All (n = 227)
%	Beneficial	65	63	63	60	61	74	60	79	56	86	94	89
	Not beneficial	18	6	6	20	7	4	5	14	12	14	6	11
	Detrimental	6	12	5	20	7	4	10	0	4	10	21	12
	Not detrimental	35	44	30	60	39	37	26	36	24	90	79	88

Note. Enrichment category percentages derived from count data of articles stating if beneficial and/or detrimental resulted were or were not present. Percentage of individual enrichment category outcomes and article total outcomes are split between articles exclusively using single enrichment categories and articles combining multiple enrichment categories. Not stated results omitted.

Discussion

Enrichment Category Study Variability

Some enrichment categories, such as feeding enrichment, have received substantially more attention in terms of publication and species representation than others (i.e., training enrichment and olfactory enrichment). This variation could exist due to three reasons. 1) The ‘file-drawer effect’, a bias in publishing only significant results (Scargle, 2000). This agrees with the finding that > 99% of published primate EE articles achieved their initial hypothesis. 2) Scientists may be more likely to investigate EE that is convenient, minimizes risk, is temporally inexpensive, and requires little implementor training. This partially explains why feeding, structural, tactile, and cognitive enrichment are overrepresented and why EE viewed as potentially hazardous or temporally taxing (e.g., training enrichment) is comparatively underrepresented. Auditory and olfactory enrichment meet the above criteria (i.e., easily manageable etc.), but they are not represented to the same degree. However, this could be due to a third reason: 3) EE is implemented based on the implementors previous understanding of primate behavioral ecology, specifically them being visually dominant animals, despite olfactory and auditory senses being used in goal seeking behavior (Carvalho et al., 2017; Heffner, 2004; Laska & Salazar, 2015; Riley & Rose 2020). Due to these reasons, research that could aid in EE implementation, increase primate welfare, and direct future research direction, may continue to be overlooked.

Understudied Enrichment Categories

The prevalence of studies on feeding and structural enrichment exceeds that of sensory or training enrichment. This discrepancy raises concerns for three reasons: 1) A deficiency of published enrichment research limits our ability to determine how an animal copes with specific environmental interventions. 2) Enrichment categories with few published articles limit understanding of their effects during a meta-analysis and therefore their effectiveness for improving wellbeing. 3) It reduces an enrichment implementors ability to utilize scientifically based enrichment that relates to the evolutionary and individual history of the animal.

Auditory Enrichment. The auditory environment presented to captive primates often deviates from their evolutionary adaptation and lacks controllability or opportunities for respite (Morgan & Tromborg, 2007). Consequently, these circumstances can induce stress, with some individuals exhibiting inadequate stress relief mechanisms, leading to compromised welfare (Morgan & Tromborg, 2007). To counteract this auditory enrichment can be used to reduce or cloak persistent external noise, encourage potentially beneficial vocal behavior using allospecific and conspecific calls, or give primates control over their auditory environment (Sekulic, 1983; Wallace et al., 2017; Watson et al., 2014; Wells, 2009). While most auditory stimuli demonstrate positive effects, certain stimuli exhibit limited or negligible impacts on primate behavior (Hanbury et al., 2009; Wallace et al., 2017; Wells et al., 2006). This mixed evidence for the efficacy of auditory enrichment, could explain why there is less emphasis on its use. However, due to the limited and occasionally inconclusive literature, replication of previous studies is needed to increase their generalizability (Khan & Wascher, 2021). Alongside this further research encompassing diverse species, an individualized approach when possible, and the addressing of specific welfare issues are required to establish definitive conclusions regarding the efficacy of auditory stimuli in enhancing primate welfare (Kriengwatana et al., 2022; Snowdon, 2021).

Olfactory Enrichment. The scarcity of published research on olfactory enrichment, as noted by Clark and King (2008), remains evident based on the findings of this review. This limited availability of data could stem from researchers prioritizing visual stimuli over those targeting the olfactory sense, despite inter-species variations in olfactory utilization (Laska & Salazar, 2015). The dearth of publications, especially from laboratories, is likely impeding our understanding of how a primate's olfactory environment correlates with stress, and the potential benefits of olfactory enrichment for enhancing welfare (Wells et al., 2007). Therefore, to facilitate the provision of optimal welfare standards for primates, further investigation into the effects of olfactory enrichment is urgently warranted.

Since olfactory sensitivity and use can differ between individuals and species, and since olfactory enrichment research is still in its infancy, it would be wise to focus on species which are known to utilize their olfactory system in the pursuit of food and social communication (Laska & Slazar, 2015). For example, squirrel monkeys (*Saimiri sciureus*), spider monkeys (*Ateles geoffroyi*), and pigtail macaques (*Macaca nemestrina*) all have excellent olfactory differentiation capabilities, and therefore would make suitable candidates for future research (Laska et al., 2000; Laska et al., 2006; Laska & Seibt, 2002; Salaza et al., 2003). While great apes (e.g., Western lowland gorilla) have also displayed odor differentiation abilities, their mixed olfaction enrichment results to-date, invite continued research (Charmoy et al., 2015; Hepper & Wells, 2012; Wells et al., 2007).

Training Enrichment. Training captive primates has traditionally been viewed as both temporally and financially expensive (Reinhardt, 1997; Rennie & Buchanan-Smith, 2006). This may explain why training enrichment is comparatively understudied. However, recent studies have demonstrated that training primates is not as time-consuming as previously believed and is increasingly being employed by laboratories and zoos (Baker, 2016; Fernandez & Martin, 2021; McKinley et al., 2003; Perlman et al., 2012; Schapiro et al., 2005). The results indicated that training enrichment could result in immense welfare benefits, and the lack of detrimental outcomes suggests that this form of EE holds potential for enhancing safety standards and primate welfare, particularly in the context of human interactions, medical procedures, facilitation of enrichment opportunities, and more, although further research is needed (Fernandez, 2022; Palmer et al., 2022; Melfi & Ward, 2020; Prescott et al., 2005).

Visual Enrichment. Most primate species have evolved trichromatic color vision, which aids their acquisition of food, and identification of social members and threats (Carvalho et al., 2017). To counteract a lack of visual stimulation within captivity, visual enrichment including brightly colored objects, mirrors, and videos are commonly provided, predator silhouettes have been used to stimulate threat identification behaviors, and recently interactive computerized visuals have been introduced (Moodie & Chamove, 1990; Wells, 2009; Yamanashi et al., 2021). However, provision continues to lack translation into extensive publication, notably from zoos (Coleman & Novak, 2017; Wells, 2009). Despite this, the results show visual enrichment benefits primates' welfare without a serious risk of detrimental outcomes. However, these results are based on only nine species and therefore more research should be undertaken on a greater diversity of species before these results can be generalized.

Species Diversity and Research Setting

Primates are the most studied taxa within enrichment evaluation publications (Alligood & Leighty, 2015; Shyne, 2006; Swaisgood & Shepherdson, 2005; Swaisgood & Shepherdson, 2006). Meanwhile within the published primate research there exists a species representation bias, with most research focused on chimpanzees and rhesus macaques, a result akin to those found in primate cognitive research (Cronin et al., 2017). This disparity could be due to three reasons: 1) research setting determining species access, 2) species charisma, and 3) human physiological similarity.

More species are represented in zoological publications than in laboratories, a variation possibly driven by structural motivations. Zoological organizations are often required to engage in endangered species conservation (Tribe & Booth, 2003). Therefore, zoo-based researchers should have greater access to diverse, and endangered, species. Meanwhile research laboratories are motivated to conduct high quality ethical science (De la Fuente et al., 2017). In their ethical workings many laboratories in western countries (e.g., United Kingdom), have banned or restricted great ape experimentation (Knight, 2008). Laboratories instead rely on monkey model species (e.g., the most recorded species the rhesus macaque) (Andrade et al., 2003; Messaoudi et al., 2011). Therefore, due to subject choice being dictated by the research settings species pool, this disparity between labs and zoos is expected.

Zoological-based EE research could benefit from its unique capacity to investigate a diverse range of species within naturalistic enclosures. However, there exists a bias in favor of conserving charismatic species, and individual zoos typically only house limited numbers of each species, with some pair bonded species potentially only being represented by two individuals at a given institution. These aspects can influence researchers to focus their efforts on populations with larger numbers, which are typically apes, and this results in limited accessibility to study less well-known primates (Colléony et al., 2017; Hopper, 2022; Small, 2012). This bias is also reflected in the published zoological EE literature, with an overrepresentation of large charismatic primates such as chimpanzees and Western lowland gorillas. To address this imbalance, future research in both zoo and laboratory settings should prioritize studying underrepresented species, while also fostering multi-institution collaborations to better facilitate access to a diverse species pool, as suggested by Hopper (2017), and demonstrated by ManyPrimates et al. (2022).

Measuring Issues

Over half of EE studies mixed their enrichment category outcomes into a single result. This limits accurate determination of which stimuli affected behavior and/or physiology. Unless future investigation is specifically testing the effects of mixed category enrichment, independent testing and result presentation of these categories should be prioritized to allow for meta-analysis and the accurate implementation of EE.

Behavioral Measures

Most EE studies rely on using behavior as the key welfare impact indicator. The use of behavioral recording methods coupled with non-behavior measures (i.e., enclosure location), provides scientists with enhanced situational adaptability, and capability to assess welfare (Altmann, 1974; Watters et al., 2021). Therefore, enrichment research could explore in depth inter-individual behavioral differences, which may enable greater individualized enrichment treatments, as discussed by Norman et al. (2021), and Robinson and Weiss (2023). While, also benefiting from advancements in behavioral technology, which are decreasing operation costs, and enabling data collection during previously inaccessible periods (Canino & Powell, 2010; Rushen et al., 2012). This has been demonstrated by Chopra et al (2020) who used a local positioning system to monitor changes in behavior potentially indicative of health concerns, in farmed dairy cattle. Zoos and laboratories should capitalize on this growing range of independent recording technologies (e.g., accelerometers, global positioning systems, radio frequency identification systems, bioacoustic measurement systems, and thermographic cameras), to assist in enrichment implementation, and welfare assessments (Whitham & Miller, 2016).

Physiological Measures

Cortisol was most used to measure stress, likely because it can be collected through non-invasive methods (e.g., fecal collection) (Heistermann, 2010). Caution should be taken when exclusively using physiological data to understand primate welfare due to individual variation in baseline cortisol levels, modulated by environment, previous experiences, and genetics (Behie et al., 2010; Cross & Rogers, 2004; Fairbanks et al., 2011; Novak et al., 2013). Additionally, rising cortisol levels do not specifically relate to poor welfare, for example sexual excitement increases cortisol while not decreasing welfare (Hohmann et al., 2009). Meanwhile, low cortisol levels do not necessarily represent good welfare, as this can induce health problems (e.g., adrenal insufficiency) (Pignatti & Flück, 2021; Novak et al., 2013).

The choice of cortisol collection method can impact the interpretation of data. Cortisol levels derived from blood and saliva samples captures a momentary snapshot, whereas urine, feces, or hair samples reflect the cumulative corticosteroid secretion over extended time frames, ranging from hours, to days, or in the case of hair, months. Additionally, it is important to acknowledge that blood and saliva sampling may be subject to circadian rhythm fluctuations and collection of these can be stress-inducing, all of which skew data if only measured once. Nonetheless, it is imperative to recognize that each sampling method presents distinct advantages and disadvantages, necessitating careful consideration within experimental design (Novak et al., 2013). However, measuring cortisol before, during and after the addition of EE, and alongside behavioral and/or other physiological measurements (e.g., body weight) has potential to better inform welfare management when customized to the individual (Hill & Broom, 2009; Mason & Mendl, 1993; Mormède et al., 2007).

Other Measures

The wide array of supplementary sampling methods underscores the versatility of utilizing enrichment-based welfare evaluations in both zoological and laboratory settings. Notably, the temporal aspects of recording time within separate 'enclosure locations' and the assessment of interpersonal distances as 'social proximity' lend themselves to the application of social network analysis. Remarkably, according to the results this analytical approach has not found utilization in primate enrichment research. Social network analysis has been demonstrated to offer valuable insights into various facets of primate social behavior. These encompass disparities in individual social tendencies, the identification of preferred conspecific associations contributing to group cohesion, discerning alterations in social interactions over time that may indicate welfare-related concerns, and the examination of resource utilization (Clark, 2011; Jacobson et al., 2019; McCowan et al., 2008; Radosevich et al., 2021; Rose & Croft, 2015). Given these promising findings, it is vital that inquiries be undertaken to assess the efficacy of social network analysis as an innovative tool for evaluating the impact of EE on welfare at the individual level, and social dynamics at the group level.

Future Directions

The evidence overwhelmingly supports the benefits of EE for primates, without significant detrimental effects, whether implemented independently or in conjunction with other enrichment strategies. These findings substantiate the utility of enrichment as a powerful tool in promoting a high standard of welfare for primates. However, these results could be due to the 'file-drawer effect'. A limitation in this paper is that descriptive statistics only provide partial information from which to understand enrichment in terms of its evolutionary relevance to each species, which is important for the successful implementation of EE (Newberry, 1995). Therefore, the next stage should be conducting a detailed meta-analysis examining each enrichment category to determine their effects, and effectiveness to improve primate welfare.

To counter the 'file-drawer effect' scientists should seek to publish all their enrichment experiments with data that is extractable, regardless of their outcome. Reports of enrichment evaluations that demonstrate no improvement to welfare should be published, and future literature reviews could also include gray literature and conference abstracts, which might be more likely to report unsuccessful EE interventions. Such an approach would result in increased availability of data on understudied enrichment categories and species. Consequently, a more comprehensive understanding of how different species adapt to specific environments and respond to various enrichment interventions can be attained. Moreover, this practice would enhance the precision and reliability of future meta-analytic studies.

Conclusion

Primate EE is a steadily progressing area of study. Nevertheless, there are considerable disparities between enrichment categories, species representation, and data useability. These issues potentially limit the implementors ability to provide the best welfare standards possible. Despite this, beneficial outcomes are reported significantly more than detrimental outcomes for all enrichment categories and conditions. This is encouraging given the extent of enrichment use within captivity, although this result could be due to the 'file-drawer effect'. These findings are provided through descriptive statistics of only freely available publications and therefore are limited evidence. Next, a meta-analysis of all published peer-reviewed primate enrichment research should be conducted to understand what welfare benefits, enrichment category effects, and functional relevance each enrichment category and item has to each species. Future research should focus on increasing data extractability, and testing novel welfare related measures (e.g., social network analysis) whilst also investigating underrepresented species, housing conditions, and enrichment categories (i.e., auditory, olfactory, social, training, and visual).

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Supplementary Material

Table S1

List of Species and Number of Articles Recorded in each Research Setting

Species	Research Setting		
	Lab	Zoo	Not stated
Barbary macaque (*Macaca sylvanus*)	0	1	0
Black capuchin (*Sapajus nigritus*)	0	1	0
Black howler (*Alouatta caraya*)	0	1	0
Black lemur (*Eulemur macaco*)	0	1	0
Black-and-white ruffed lemur (*Varecia variegate*)	0	1	0
Black-capped squirrel monkey (*Saimiri boliviensis*)	2	2	0
Black-striped capuchin (*Sapajus libidinosus*)	0	2	0
Black-tufted marmoset (*Callithrix penicillate*)	1	0	1
Blue-eyed black lemur (*Eulemur flavifrons*)	0	1	0
Bonnet macaque (*Macaca radiata*)	3	0	0
Bonobo (*Pan paniscus*)	0	1	0
Bornean orangutan (*Pongo pygmaeus*)	6	0	0
Chimpanzee (*Pan troglodytes*)	27	13	0
Collared brown lemur (*Eulemur collaris*)	0	1	0
Collared mangabey (*Cercocebus torquatus*)	1	0	0
Colombian white-faced capuchin (Cebus capucinus)	2	0	0
Common brown lemur (*Eulemur fulvus*)	0	1	0
Common marmoset (*Callithrix jacchus*)	10	1	1
Coquerel's sifaka (*Propithecus coquereli*)	0	1	0
Cotton-top tamarin (*Saguinus oedipus*)	2	3	0
Crab-eating macaque (*Macaca fascicularis*)	7	1	0
Crowned lemur (*Eulemur coronatus*)	0	1	0
Diana monkey (*Cercopithecus diana*)	0	1	0
Drill (*Mandrillus leucophaeu*)	0	2	0
Geoffroy's spider monkey (Ateles geoffroyi)	0	0	1
Goeldi's marmoset (*Callimico goeldii*)	0	1	0
Golden lion tamarin (*Leontopithecus rosalia*)	0	1	0
Golden-headed lion tamarin (*Leontopithecus chrysomelas*)	0	1	0
Gray slender loris (*Loris lydekkerianus*)	0	1	0
Grey-cheeked mangabey (*Lophocebus albigena*)	0	0	1
Grivet (*Chlorocebus aethiops*)	3	2	0
Guianan squirrel monkey (*Saimiri sciureus*)	3	5	0
Guinea baboon (*Papio papio*)	1	0	0
Hamadryas baboon (*Papio hamadryas*)	3	2	0
Japanese macaque (*Macaca fuscata*)	5	1	0
Javan slow loris (*Nycticebus javanicus*)	0	2	0
Lar Gibbon (*Hylobates lar*)	0	2	0
Lion-tailed macaque (*Macaca silenus*)	0	2	0
Mandrill (*Mandrillus sphinx*)	0	3	0
Mantled guereza (*Colobus guereza*)	0	1	0
Mona monkey (*Cercopithecus mona*)	0	1	0
Moustached guenon (*Cercopithecus cephus*)	0	1	0
Northern greater galago (*Otolemur garnettii*)	1	0	0
Northern plains gray langur (*Semnopithecus entellus*)	0	1	0
Northern white-cheeked gibbon (*Nomascus leucogenys*)	0	2	0
Olive baboon (*Papio Anubis*)	3	0	0
Patas monkey (*Erythrocebus patas*)	1	0	0
Philippine slow loris (Nycticebus menagensis)	0	1	0
Pied tamarin (*Saguinus bicolor*)	0	1	0
West African potto (*Perodicticus potto*)	0	1	0

Species	**Lab**	**Zoo**	**Not stated**
Western pygmy marmoset (*Cebuella pygmaea*)	0	1	0
Red ruffed lemur (*Varecia rubra*)	0	2	0
Rhesus macaque (*Macaca mulatta*)	56	1	0
Ring-tailed lemur (*Lemur catta*)	0	7	1
Senegal bushbaby (*Galago senegalensis*)	0	1	0
Siamang (*Symphalangus syndactylus*)	0	1	0
Silvery gibbon (*Hylobates moloch*)	0	3	0
Sooty mangabey (*Cercocebus atys*)	1	0	0
Southern pig-tailed macaque (*Macaca nemestrina*)	4	0	0
Stump-tailed macaque (*Macaca arctoides*)	3	2	0
Sulawesi crested macaque (*Macaca nigra*)	0	1	0
Sumatran orangutan (*Pongo abelii*)	0	4	0
Sunda slow loris (*Nycticebus coucang*)	0	1	0
Tonkean macaque (*Macaca tonkeana*)	0	1	0
Tufted capuchin (*Sapajus apella*)	3	6	0
Western lowland gorilla (*Gorilla gorilla gorilla*)	0	17	0
White-faced saki (*Pithecia Pithecia*)	0	1	0
White-headed lemur (*Eulemur albifrons*)	0	1	0
White-headed marmoset (Callithrix geoffroyi)	0	1	0
White-lipped tamarin (*Saguinus labiatus*)	0	2	0
Wolf's mona monkey (*Cercopithecus wolfi*)	0	1	0