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REVIEW

A systematic review of sex differences in rough and tumble play across non-human mammals

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Abstract

It is widely believed that juvenile male mammals typically engage in higher rates of rough and tumble play (RTP) than do females, in preparation for adult roles involving intense physical competition between males. The consistency of this sex difference across diverse mammalian species has, however, not yet been systematically investigated, limiting our current understanding of its possible adaptive function. This review uses narrative synthesis to (i) evaluate the ubiquity of male-biased RTP across non-human mammals, (ii) identify patterns of variation within and between taxonomic groups, and (iii) propose possible predictors of variation in these differences, including methodological and socio-ecological factors, for investigation by future studies. We find that most species studied do exhibit higher rates or RTP in males than females, while female-biased RTP is rare. Sex differences are smaller and less consistent than expected, with many studies finding similar rates of RTP in males and females. We identify multiple potential socio-ecological predictors of variation in sex differences in RTP, such as intrasexual competition and dietary niche. However, variation is not strongly phylogenetically patterned, suggesting that methodological and environmental factors, such as sample size and play partner availability, are important to consider in future comparative analyses.

Significance statement

Rough and tumble play (RTP) is thought to be vital for developing physical skills necessary for aggressive competition in adulthood, explaining an apparently widespread sex difference in RTP in mammals whereby immature males are more likely to engage in this behaviour than females. However, no prior study has systematically investigated the extent to which a male bias in RTP is consistent across diverse mammalian species. We find that although RTP is commonly male biased, findings were highly variable both within- and between-species, and equal participation in RTP by males and females is more common than widely assumed. Our review suggests several potential predictors of variation in sex differences in RTP, particularly levels of intrasexual competition in both males and females. However, our findings also suggest the importance of considering methodological in addition to socio-ecological factors for future research.

Keywords Systematic review · Non-human mammal · Life history · Rough and tumble play · Social play · Sex differences

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Introduction

Rough and tumble play (RTP) is a common behaviour in mammals, consisting of physically active social behaviours such as chasing and playfighting (Burghardt 2005). Typically in RTP, threats are absent, animals signal via play faces or vocalisations that they are not acting aggressively, roles frequently reverse, and sequences of constituent behaviours vary (Fry 2005). The actions involved in RTP of juveniles are similar to those exhibited by adults in “serious” contexts of competitive, aggressive, and social encounters (Panksepp et al. 1984), which, together with specialised behaviours to communicate benign intent, suggests that RTP in early life is used to develop skills for social and environmental challenges in adult life (Norscia and Palagi 2016).

Variation in sex differences in RTP across species could shed light on evolutionary drivers of play, but has not yet been systematically investigated. In mammals, it is generally believed that juvenile males typically engage in higher levels of RTP than females (Graham and Burghardt 2010), which has been linked to adult behavioural sex differences in physical aggression and competition; male mammals generally engage in more fighting, dominance, and defence behaviours than females (Paukner and Suomi 2008). In contrast, immature females are considered more likely to invest in lower intensity forms of RTP (Berghänel et al. 2015), or other social behaviours such as grooming (Young et al. 1982). One source of evidence suggesting that RTP should be male-biased concerns the role of androgens, which have been demonstrated to influence behaviours and “masculine” traits such as aggression, dominance, and RTP (Grebe et al. 2019). However, there are indications that higher levels of RTP in males than females may not be distributed as expected, and variation may correlate with socioecological factors (Smaldino et al. 2019). For example, frequent, high-intensity female RTP may also be expected for species with high levels of female-female competition, a possibility that has so far been largely overlooked (Stockley and Campbell 2013). Our ability to propose well-informed hypotheses concerning the evolutionary origins of RTP would therefore be improved by first establishing the phylogenetic distribution of sex differences, which is currently unknown.

Proposed adaptive functions of RTP

Life history theory posits that growth rates, age and size at sexual maturity, and reproductive investment are shaped by natural selection to maximise reproductive success (Emery Thompson 2017; Stearns 2000). Due to sex differences in type and extent of investment required for reproduction, male and female mammals typically differ in their mating/reproductive strategies (Gittleman and Thompson 1988; Pontzer 2015). Male mammals typically bear high costs of intrasexual competition to secure mates and maximise reproductive potential, whereas females bear costs of gestation and lactation, investing more time and energy in individual offspring (Key and Ross 1999; Kokko and Jennions 2008). Typically, it is argued that males are more likely to invest in and bear the costs of RTP to maximise their competitive ability and reproductive success in later life, whereas females focus on early maturation to maximise time spent reproducing (Charnov 1991). This hypothesis emphasises the importance of juvenile RTP for the development of motor control (Byers and Walker 1995), and muscular strength (LaFreniere 2011), both of which would aid in adult intrasexual competition. However, so far this idea has not considered variation in the extent to which adult males and females invest in mating competition or parental care across species (Clutton-Brock et al. 2006).

RTP may also be crucial preparation for dominance interactions over other resources, such as food, and to build alliances, both during immaturity and in adulthood (Maestripieri and Ross 2004). If so, sex differences in RTP should depend on the social system and foraging ecology of the species, as these affect the importance of aggressive competition in the two sexes. According to this hypothesis, sex differences in RTP are not expected when adult males and females have similar social and foraging behaviours. This may be the case in some carnivorous species, for example, where developing hunting skills through play is of equal importance to males and females (Lewis 2003). Similarly, we may expect minimal sex differences in RTP where adult males and females both require sophisticated social skills, as communication of intent is a fundamental component of RTP (Palagi et al. 2016). Quantifying the extent of variation in sex differences in RTP across mammalian species is, however, required before such hypotheses can be formally developed and tested in comparative analyses.

Energy constraints and sex differences in RTP

Energetic trade-offs may also be important for understanding variation in sex differences in RTP both across and within species. Life history theory concerns how animals allocate energy over the lifespan in order to maximise fitness (Emery Thompson 2017). Energy can be used for maintenance and repair, growth, or reproduction, and males and females are likely to differ in how they invest the energy they harvest from the environment as they have different energy requirements for reproduction and maintenance (Hill 1993; Lappan 2009). Energy budgets can be affected by environmental and seasonal factors, and variation in the availability of food sources has direct effects on energy intake (Emery Thompson 2017). This could affect within-species variation in time spent in RTP, as animals reduce time spent in play when resources are scarce (Krachun et al. 2010; Held and Špinka 2011). Under such conditions, RTP rates should be conserved in the sex for whom it has most direct fitness benefits, or the sex where it contributes greater survival benefits. As animals are unlikely to experience constraints on food availability in captivity (Howell and Cheyne 2019), sex differences should therefore be less pronounced in captive groups. However, females may still continue to invest in growth and early reproduction, which can lead to earlier reproduction and obesity in captive females (Charnov 1991), which may also affect rates of RTP.

Objectives of the systematic review

We undertook a systematic review to investigate the within- and across-species variation in sex differences in RTP in non-human mammals. The aims of the review were to (i) evaluate the ubiquity of male-biased RTP in non-human mammals; (ii) identify variation in sex differences in RTP within and across taxonomic groups; and (iii) highlight potential biological, social, ecological, contextual, and methodological factors underlying variability in sex differences in RTP to be investigated by future studies. We used narrative synthesis (Popay et al. 2006) to summarise the literature and identify variables that may be associated with sex differences, with a focus on factors relevant to life history and sexual selection including mating system, sexual size dimorphism, male competition, dispersal, and sexual segregation. Employing narrative synthesis allowed us to assess quantitative and qualitative evidence, including the quality and variation of methodology (Howell and Cheyne 2019). This is particularly relevant to studies on play, which can be highly methodologically heterogenous. Play can be measured by rates, initiations, and time budgets, and studies of play also vary widely in sample sizes, contexts, and statistical approaches, all of which can be evaluated holistically using narrative synthesis. Where possible, we complemented qualitative discussion of patterns in the literature with quantitative analyses, including an analysis of taxonomic bias (Clark and May 2002) to assess the extent to which data were biased towards specific mammalian orders due to greater research interest, and a comparison of sample sizes between studies with different findings to see if unusual findings were more common in lower-powered studies.

Methods

Pre-registration

A protocol for the systematic review methodology was pre-registered using the Open Science Framework (see Foster and Deardorff 2017), to ensure that the research is credible, transparent, and replicable (https://osf.io/a2q98/).

Information sources

Sources were identified using Scopus, Web of Science (Core Collection and Zoological Record), and ProQuest (Dissertations & Theses). Further texts were identified by searching reference lists of relevant results. Sources of information were all identified in April 2021.

Search strategy

For RTP, the following search terms were selected: “social play”, “play activit*”, “play fight”, “play pattern”, “play behav*”, “rough and tumble”, “wrestling”, “play partner”, “playmate”, “play solicit*”, “playful interact*”, “aggressive play”, and “play and playthings”. Search terms were selected by identifying key words which were used to refer to RTP in the known literature, other than “play and playthings”, which was suggested by Scopus. The terms “play”, “social interactions”, and “social behaviour” were excluded as they introduced large numbers of irrelevant results. A term for “sex differences” was not included as studies were often not tagged as such, which may unintentionally exclude relevant results.

For Scopus, Web of Science Core Collection, and ProQuest, results were limited to non-human animals with the terms “nonhuman”, “non-human”, “animal*”, “juvenile”, “infant”, “yearling”, “young”, “immature”, or “species”, and excluding the term “child*”. Excluding “human” resulted in many relevant studies being excluded, so the term “child*” was used as an alternative. For the Zoological Record, these terms were not used, as the database only contains non-human studies. As RTP is rare in non-mammalian animals and the literature has focused on RTP in mammals (Burghardt 2005), specific non-mammalian species were not excluded using filters, as few results were expected and could be removed manually. See Table 1 for the final search strategies.

Additional sources were identified by searching the reference lists of eligible papers identified by these searches, as well as those of other relevant sources such as review papers.

Table 1 Search strategies

Database	Search strategy	Number of results
Scopus	TITLE-ABS-KEY ((“social play” OR “play activit*” OR “play fight*” OR “play pattern*” OR “play behav*” OR “rough and tumble” OR wrestling OR “play partner” OR playmate OR “play solicit*” OR “playful interact*” OR “aggressive play” OR “play and playthings”) AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) AND NOT (child* OR lab OR laboratory))	2468
Web of Science Core Collection	TS = ((“social play” OR “play activit*” OR”play fight*” OR”play pattern*” OR”play behav*” OR”rough and tumble” OR wrestling OR”play partner” OR playmate OR”play solicit*” OR”playful interact*” OR”aggressive play” OR”play and playthings”) AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) NOT (child* OR lab OR laboratory))	1339
Web of Science Zoological Record	TS = ((“social play” OR”play activit*” OR”play fight*” OR”play pattern*” OR”play behav*” OR”rough and tumble” OR wrestling OR”play partner” OR playmate OR”play solicit*” OR”playful interact*” OR”aggressive play” OR”play and playthings”) NOT (child* OR lab OR laboratory)) AND (ST = mammalia)	509
ProQuest	(“social play” OR (“play activities” OR “play activity”) OR (“play fight” OR “play fighting”) OR (“play patterns”) OR (“play behavior” OR “play behaviour”) OR “rough and tumble” OR wrestling OR “play partner” OR playmate OR “play solicit*” OR “playful interact*” OR “aggressive play” OR “play and playthings”) AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) NOT (child* OR lab OR laboratory)	1992

Eligibility criteria

Texts were deemed relevant if they contained comments or data on intraspecific RTP carried out by non-adult members of a species, which was split by sex, or the authors had carried out a statistical test which identified if sex had a significant effect on level of RTP. Texts were limited to those focusing on play between peers, as mother-infant play, or play with other adult members of a group may have different functions to RTP with same-age peers. This resulted in exclusion of some studies that focused on infants, as the majority of their play is with the mother. Texts were excluded if they did not contain relevant data, were not written in English, concerned interspecific or adult-only play, involved animals that had undergone experimental or physical manipulation or were placed into pairs for observation, or had definitions of RTP that included aggression and/or individual play. For synthesis, studies were grouped by mammalian order, and further by family for the primates given the large number of studies identified from this order.

Selection process

Texts identified as potentially relevant were first screened by title and abstract, and then by reading the full paper. The process was mostly carried out by the first author, with discussion between authors for difficult cases. The selection process was carried out using Covidence software (Veritas Health Innovation 2019).

Data collection

Data were collected by the first author. Any data that matched the inclusion criteria were recorded, including data collected at multiple time points and/or for different groups. Information was recorded in a spreadsheet, where additional information on Author, Year Published, Document Type, Journal/Book Name, Title, Species, Order, Location, Habitat, Sample Information, Age, Sexual Dimorphism, Mating System, Social System, Diet, Definition of RTP, Method, Duration of Study, Captive/Wild, Results, Analysis, Direction of Sex Difference in RTP, and General Notes was included. No assumptions were made for any missing or unclear information.

Taxonomic bias

A potential source of literature bias particularly relevant to the present study is taxonomic bias, in which certain species attract more research than is proportionate to their frequency in nature (Clark and May 2002). Research effort may be influenced by how easy it is to observe a species, which traits are of interest, and/or phylogenetic position (Ducatez and Lefebvre 2014). The bias introduced by research effort is reinforced by taxonomic chauvinism, in which papers concerning “unpopular” species are less likely to be published due to perception of less interest (Bonnet et al. 2002).

We carried out an analysis of taxonomic bias using a permutation approach (as used in e.g. Blackburn and Cassey 2007), to test for differences between the observed number of species in each order with data on RTP, and the number that would be expected if the sample was representative of mammalian diversity (Supporting Information). We took 10,000 random samples of mammalian species of the same size as the sample with data on RTP, to compare the number of species with RTP information in each order against the number that would be expected without taxonomic bias. For each iteration of the simulation, samples of 66 species (representing the sample size included in the systematic review) were chosen at random, without replacement, from the total number of mammalian species, and the sum of species chosen for each order was calculated, which represented the expected value. Medians and 95% intervals were then computed for the expected number of mammals in each order across the samples, to judge if the observed number of species within each order was significantly different from that expected under random sampling.

Sample size

To analyse the extent to which the sample size of a study could bias the findings, we compared the sample size of studies between those finding male-biased RTP, female-biased RTP, and no sex differences. We were particularly interested to see whether studies reporting rarer outcomes were more likely to have smaller samples and therefore a greater risk of spurious findings. Since data did not meet parametric assumptions, we used a Kruskal–Wallis test to compare median sample sizes between the three groups.

Effect measures

For each study, the direction of sex differences in RTP was recorded; this could be in the form of effect sizes, significance tests, reporting of group means and/or frequencies, or verbal summaries, where available. If results were split by age, population, time, or specific behaviour (e.g. split into chasing or wrestling) this was also recorded.

Synthesis methods

Texts were grouped by mammalian order for narrative synthesis. Within each order, studies were initially grouped by their findings (male bias, female bias, or no sex difference). Then, common characteristics of species were identified within these groups, to identify potential predictors of sex differences in RTP for investigation in future comparative analyses. The strength of evidence for sex differences was assessed qualitatively based on sample size, setting, age range of study animals, and rigor of statistical testing, with more weight given to studies that were deemed higher quality. Results were summarised in tables, including information on these methodological categories. Quantitative synthesis (e.g. meta-analyses) could not be carried out due to high methodological heterogeneity between the studies, particularly in terms of the definitions and measures of RTP.

Results

Study selection

The systematic search initially found 4970 results after duplicates were removed, which were screened by title and abstract, identifying 549 sources for full-text screening. We could not access 22 studies, which were excluded at this stage. 452 results were excluded as the full text did not meet the criteria. Exclusion criteria were the following: the text did not contain relevant data, was not written in English, concerned interspecific or adult-only play, involved animals that had undergone experimental or physical manipulation, involved animals that were placed into pairs for observation, or had definitions of RTP that included aggression and/or individual play. The majority of papers that were excluded were unsuitable due to animals having undergone experimental manipulations such as hormone treatments or gonadectomies. Ninety-seven texts were deemed relevant from the initial systematic search. One hundred thirteen further texts were identified through reference list searching, 22 of which were suitable for inclusion. Two further sources were identified by study referees. Thus, a total of 121 sources were included for narrative synthesis. See Fig. 1 for a flow chart of the screening process.

Sources of data ranged from the year 1967 to 2020 and consisted of 104 journal articles, 4 book chapters, 1 meeting abstract, and 10 theses. Seventy-three of these sources contained data on primates, 16 on carnivora, 11 on artiodactyla, 10 on rodentia, 5 on perissodactyla, 2 on proboscidea, and 1 each for chiroptera, dasyuromorphia, and diprotodontia.

Fifty-nine studies showed a male bias in RTP, 3 studies a female bias, and 41 reported no sex differences in RTP. All studies concerned RTP, but some looked at specific component behaviours of RTP. For example, some studies such as Fragaszy et al. (2004) and Paukner and Suomi (2008) make a distinction between sub-types of RTP, such as wrestling and chasing. Other studies specify a particular measure of RTP, such as initiations, rates, or total times. Although all discussed results concern RTP, we have maintained the use of the phrases used in each study so that results cannot be misconstrued or over-generalised. Where measurements of RTP concern rates and/or durations, we have made the distinction clear, and do not weigh one in favour of the other.

Sixty-one percent of studies were on captive populations, 36% wild, and 3% wild but provisioned. For studies that reported sample size, samples ranged from 3 to 213

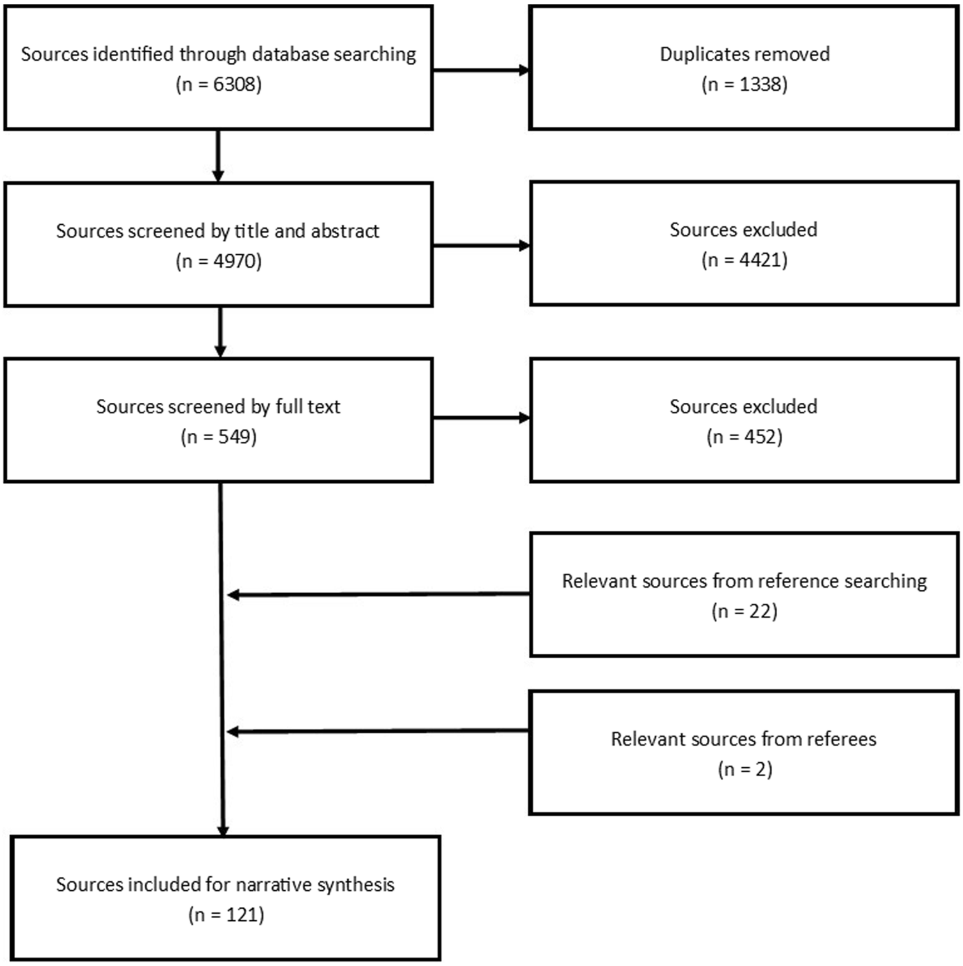

Fig. 1 Screening process showing stages of exclusion

individuals, with a median value of 18. The median sample size was 15 for captive groups, 27 for wild, and 20 for provisioned. Further details and a summary of the results of each text can be found in Table 2, and the phylogenetic distribution of results is shown in Fig. 2. Figure 3 shows the distribution of results by order.

Taxonomic bias

As seen in Fig. 4, primates were hugely overrepresented within the sample ($p < 0.05$), with 33 relevant species, compared to the five predicted based on the size of the primate order. Other significantly over-represented orders ($p < 0.05$) included the carnivora (11 relevant species compared to 3 predicted) and the proboscidea (2 relevant species compared to 1 predicted). The dasyuromorphia, diprotodontia, and perissodactyla were represented in line with expectations, not differing significantly from the expected value.

Most other orders were under-represented, most notably the rodentia (with 8 relevant species compared to a predicted 27), and the chiroptera (with 1 relevant species compared to a predicted 15) ($p < 0.05$). Eighteen mammalian orders were not represented at all within the sample.

Sample size

The sample size for studies that showed a female bias in RTP was lower than those that showed a male or no bias, with medians of 9.5, 18, and 19 respectively (Fig. 5). However, a Kruskal–Wallis test showed that these differences were not statistically significant, $H(2) = 2.2051$, $p = 0.332$. This suggests that findings were unlikely to be biased by sample size of the individual study.

Artiodactyla (even-toed ungulates)

Artiodactyla is one of the most diverse orders of mammals, consisting of primarily omnivorous or specialised herbivores (Macdonald 2014). There tends to be male-biased sexual dimorphism in artiodactyl species, which is associated with sexual segregation, sex differences in habitat use, polygynous mating systems, and high levels of male competition

Table 2 Summary of results

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
Artiodactyla	Domestic pig, *Sus scrofa*	Dobao et al. 1985	50–68 days	18 days (130 min per individual)	32	Mean number of play bouts	○		
		Brown et al. 2018	0–8 weeks	8 weeks	83	Social play	●		
		Brown et al. 2015	1 week to weaning	1 week to weaning age	70	Total social play behaviours	●		
	Siberian ibex, *Capra ibex sibirica*	Byers 1977	Immature	> 50 h	14	Total social play patterns	●		
		Byers 1980	Immature	–	20	Initiation of social play bouts	○		
	Cuvier's gazelle, *Gazella cuvieri*	Gomendio 1988	Immature	8 months	16	Play-fighting	●		
	Scimitar-horned oryx, *Oryx dammah*	Pfeifer 1985	Immature	135 days (644 h total)	8	Number of social play bouts	●		
						Duration of social play bouts			●
	Bighorn sheep, *Ovis canadensis*	Hass and Jenni 1993	Juveniles	27 months (635 h total)	10	Rate of play	●		
	Domestic sheep, *Ovis aries*	Sachs and Harris 1978	0–10 weeks	Two lambing seasons	147	Reciprocal Butting			●
						One-way butting	●		
						Mounting	●		
	Black-tailed deer, *Odocoileus hemionus columbianus*	Miller 1975	Yearlings and fawns	5 months (1411 h total)	15	Chasing			○
	White-lipped peccary, *Tayassu pecari*	Nogueira et al. 2011	Juveniles and sub-adults	12 weeks (160 h total)	12	Number of social play interactions		●	
Carnivora	Grey seal, *Halichoerus grypus*	Cairns 2013	6 months to 5 years	3 breeding seasons	10	Mean level of social play			■
		Surviliene et al. 2016	Juveniles and sub-adults	3 months (107 h total)	-	Number of dyadic play bouts	□		
	South American fur seal, *Arctocephalus australis*	Harcourt 1991	1 to 25 months	1 year (2523 h total)	36	Play			■
	Harbour seal, *Phoca vitulina*	Renouf and Lawson 1987	–	3 months (> 70 h)	Approximately 300	Chasing			■
	Galapagos fur seal, *Arctocephalus galapagoensis*	Arnold and Trillmich 1985	18–37 days	3 months	6	Length of playfighting bouts	□		

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
	Dog, *Canis familiaris*	Lund and Vestergaard 1998	0–8 weeks	8 weeks	22	Initiations of social play	●		
		Ward et al. 2008	3–40 weeks	7.1 h	19	Initiations of play in mixed-sex dyads	●		
		Koscinczuk et al. 2015	40–45 days	–	32	Social play activity			●
		Pal 2010	0–12 months	1 year	24	Initiations of play fighting	■		
		Pal 2008	0–4 months	1 year	35	Frequency of social play per hour	■		
	Coyote, *Canis latrans*	Vincent and Bekoff 1978	20–35 days	15 days (180 h total)	4	Frequency of play	○		
	Wolf, *Canis lupus occidentalis*	Cafazzo et al. 2018	3–5 months	15.6 h	12	Competitive social play			○
						Relaxed social play			○
	Eurasian lynx, *Lynx lynx*	Antonevich et al. 2019	30–90 days	1654 h	50	Contact social play			●
		Alekseeva et al. 2014	30–90 days	1491 h	46	Social play			●
	Far-Eastern wild cat, *Prionailurus bengalensis euplilurus*	Antonevich et al. 2019	30–90 days	582 h	14	Contact social play			●
	Domestic cat, *Felis catus*	Antonevich et al. 2019	30–90 days	479 h	37	Contact social play			●
		Caro 1981	1–12 weeks	8 weeks	21	Social play			○
	Meerkat, *Suricata suricatta*	Sharpe and Cherry 2003	4–10 weeks	16 months	40	Rate of social play			▲
	Bush dog, *Speothos vanaticus*	Biben 1983	3–6 weeks and 15–18 weeks	150–200 min per week	12	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●
	Maned wolf, *Chrysocyon brachyurus*	Biben 1983	3–6 weeks and 15–18 weeks	150–200 min per week	8	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●
	Crab-eating fox, *Cerdocyon thous*	Biben 1983	3–6 weeks and 15–18 weeks	150–200 min per week	9	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
Primates	Ring-tailed lemur, *Lemur catta*	Gould 1989, 1990	0–16 weeks	6 months (260 h)	11	Social play			☐
		Meredith 2018	0–23 months	–	53	Time spent in social play			☐
		Grebe et al. 2019	3–30 months	315 h	18	Rates of play initiation			●
	Black-handed spider monkey, *Ateles geoffroyi*	McDaniel 1994	Infants and juveniles	8 months	31	Number of play bouts	☐		
						Involvement in play bouts	☐		
	Howler monkey, *Alouatta pigra*	Rizzo 2004	Infants and juveniles	4 months (2021 h)	-	Time spent playing			☐
	Mantled howler monkey, *Alouatta palliata*	Zucker and Clarke 1992	0–80 weeks	22 months (529.2 h)	7	Number of play bouts		☐	
	Marmoset, *Callithrix jacchus*	Box 1975	143–291 days	–	6	Play	○		
	Saddle-backed tamarin, *Saguinus fuscicollis*	Vogt 1978	–	14 months	-	Play		○	
	Capuchin, *Cebus apella*	Fragaszy et al. 2004	Infants and juveniles	–	18	Wrestling	○		
						Chasing	○		
						Overall social play	○		
		Visalberghi and Guidi 1998	12–60 months	3 months	9	Play			○
		Paukner and Suomi 2008	2 to 5 years	5 months (132 h)	11	Wrestling	●		
						Chasing	●		
		Welker et al. 1987	0 to 6 months	6 months	14	Frequency of social play behaviour	●		
		Welker et al. 1990	6 to 12 months	–	15	Frequency of social play behaviour	●		
	Squirrel monkey, *Saimiri sciureus*	Biben 1986	Approx. 10 months	5 months	10	Rate of social play	●		
						Social play bout duration	●		
		Biben 1989	9 to 15 months	40 h per individual	28	Rate of play	○		

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
	Coppery titi monkey, *Callicebus cupreus*	Chau et al. 2008	0 to 6 months	6 months	10	Contact play			●
						Chasing			●
						Tail pulling			●
	Japanese macaque, *Macaca fuscata*	Eaton et al. 1985	0 to 1 year	1 year	22	Frequency of social play	●		
		Eaton et al. 1986	1 to 2 years	3 months	18	Frequency of social play	●		
		Glick et al. 1986	12 to 24 months	5 months	18	Frequency of social play	●		
		Petit et al. 2008	1.5 to 5 years	4 months	20	Frequency of wrestling bouts	●		
						Duration of wrestling bouts	●		
						Hourly frequency of social play			●
		Koyama 1986	< 5 years	6 months	125	Frequency of chasing	■		
						Frequency of wrestling	■		
		Nakamichi 1989	0 to 4 years	4 years (656 sessions)	20	Median percentage of time spent in social play	☐		
		Shimada and Sueur 2018	1 to 4 years	2 seasons (322.9 h)	11	Ratio of time spent in social play			■
	Rhesus macaque, *Macaca mulata*	Wooddell et al. 2017	1 to 5 months	5 months (37 h)	17	Initiations of social play	■		
						Frequency of social play	■		
		Lovejoy and Wallen 1988	12 to 16 months	12 weeks (5 h per individual)	11	Initiating social play	●		
						Receiving social play	●		
		Gard and Meier 1977	8 to 30 months	8 weeks	11	Social and rough play	○		
		Yanagi and Berman 2017	< 4 years	10 months (344 h)	20	Number of play bouts	▲		
						Initiation of play bouts			▲

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
						Duration of play bouts			▲
		Ehardt and Bernstein 1987	< 5.5 years	484 observations	> 68	Social play (infants)			●
						Social play (juveniles)	●		
		Hinde and Spencer-Booth 1967	0 to 2.5 years	2.5 years	16	Active social play			○
						Passive social play			○
		Tartabini 1991	3 to 6 months	3 months	17	Initiations of play			●
	Stumptail macaque, *Macaca arctoides*	Bernstein 1980	Infants	4 years	31	Play	●		
		Nieuwenhuijsen et al. 1988	–	> 1000 h	-	Frequency of social play	○		
	Crested macaque, *Macaca nigra*	Petit et al. 2008	1.5 to 5 years	2 months	10	Hourly frequency of play			●
						Frequency of wrestling	●		
						Duration of play sessions	●		
	Common baboon, *Papio cynocephalus*	Young and Hankins 1979	0–3 months	> 128 h	25	RTP			●
		Cheney 1978	0 to 48 months	–	20	Time spent in play			☐
	Hamadryas baboon, *Papio hamadryas*	Leresche 1976	11 to 37 months	2.5 months (> 170 h)	4	Dyadic play	○		
	Olive baboon, *Papio Anubis*	Chalmers 1980	1 to 52 weeks	6 months	40	Median percentage of mouth-and-wrestle play	▲		
		Owens, 1975a/b	–	13 months	-	Social play			■
						Aggressive play	■		
	Gelada, *Theropithecus gelada*	Mancini and Palagi 2009	Non–adult	6 months (513 h)	11	Frequency of contact play			●
						Initiation of play sessions			●
		Barale 2015, Barale et al. 2015	0 to 6 years	2 years (820 h)	74	Time spent in social play	■		

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
	Vervet monkey, *Cercopithecus aethiops*	Raleigh et al. 1979	Infants and juveniles	4 months (15 hper individual)	11	Rate of RTP	●		
		Fedigan 1972	1 to 4 years	–	10	Aggressive play	●		
		Govindarajulu et al. 1993	0 to 30 weeks	8 months	7	Play frequency			■
		Bramblett 1978	Subadults	–	18	Mean rate of social play at months 1–47	●		
						Mean rate of social play at month 48–61		●	
	Sooty mangabey, *Cercocebus atys*	Bernstein 1976	Non–adults	3 years	-	Play	●		
	Samango monkey, *Cercopithecus mitis erythrarchus*	Macleod 2000	Infants and juveniles	2 years (1506 h)	27	Play	■		
	Talapoin, *Miopithecus talapoin*	Wolfheim 1977	1 to 3 years	1 year (117 h)	7	Social play	●		
	Patas monkey, *Erythrocebus patas*	Rowell and Chism 1986	1 to 3 years	–	20	Social play	●		
						Duration of play bouts	●		
						Chasing	●		
	Redtail monkey, *Cercopithecus ascanius*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	RTP	■		
	Sichuan snub-nosed monkey, *Rhinopithecus roxellana*	Li et al. 2011	Infants	11 months	7	Play	△		
	Blue monkey, *Cercopithecus mitis stuhlmanni*	Förster and Cords 2005	0 to 6 months	8 months	12	Proportion of RTP	■		
						Bout duration	■		
						Proportion of chasing		■	
	Grey-cheeked mangabey, *Lophocebus albigena*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			□

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
	Black-and-white colobus monkey, *Colobus guereza*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			☐
	Red colobus monkey, *Procolobus rufomitratus*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			☐
		Worch 2010	Infants, juveniles, subadults	1 year	37	Amount of RTP			■
	Gorilla, *Gorilla gorilla*	Brown 1988	7 to 15 years	91 h	12	Preference for RTP			○
		Mallavarapu 2002	2 to 4 years	–	5	Time spent in social play			●
		Maple and Zucker 1978	0 to 14 years	–	7	Engagement in RTP			○
		Gomez 1988	15–24 months	16 observation sessions	4	Play	○		
		Palagi et al. 2007	Juvenile	5 months (1103 h)	10	Gentle social play			●
						Mean hourly frequency of rough social play	●		
		Hoff et al. 1981	0 to 18 months	–	3	Active social play	○		
						Moderate social play			○
	Chimpanzee, *Pan troglodyte*	Bloomsmith et al. 1994	Juveniles and adolescents	154 weeks (792 h)	21	Social play	○		
		Nadler and Braggio 1974	29 to 56 months	3 months	8	Proportion of RTP	●		
		Moebius et al. 2019	Infants	3567 h	20	Social play	○		
		Hayaki 1985	Juveniles and adolescents	384 h	9	Frequency of RTP	☐		
		Markus and Croft 1995	< 7 years	4 months (6 h per individual)	12	Frequency of RTP	○		
		Montedoro et al. 2017	< 15 years	–	-	Time spent in social play	☐		
		Spijkerman et al. 1994	0 to 10 years	3 years (3120 h)	90	Amount of play (adolescents)	●		
						Amount of play (younger age classes)			●

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
		Spijkerman et al. 1996	0 to 10 years	3 years (3120 h)	90	Duration of wrestling bouts	●		
						Tickling (below 3 years)		●	
		De Lathouwers and Van Elsacker 2006	5 to 56 months	3 years	8	Time spent in social play			●
		Mendoza-Granados and Sommer, 1995	Immature	4 months (154 h)	11	Chasing	●		
						Frequency of play bouts			○
						Duration of play bouts			○
		Pusey 1990	Juveniles and adolescents	–	13	Rate of play			☐
	Bonobo, *Pan paniscus*	De Lathouwers and Van Elsacker 2006	Infants	3 years	8	Time spent in social play			●
	Orangutan, *Pongo sp.*	Nadler and Braggio 1974	29 to 56 months	3 months	5	Proportion of RTP	●		
						Chasing			●
		Maple and Zucker 1978	0 to 21 years	–	20	RTP			○
	Sumatran orangutan, *Pongo abelii*	Frohlich et al. 2020	Infants	7 years (4297 h)	4	Social play			■
		Kunz 2015	2 to 14 years	6 months	-	Social play			■
	Bornean orangutan, *Pongo pygmaeus wurmbii*	Frohlich et al. 2020	Infants	7 years (4297 h)	7	Social play			■
		Kunz 2015	2 to 14 years	6 months	-	Social play			■
Rodentia	Prairie vole, *Microtus ochrogaster*	Chau et al. 2008	20 to 50 days		40	Total play rate			●
	Capybara, *Hydrochoerus hydrochaeris*	Congdon 2007	Juvenile, subadult	15 months (1180 h)	-	Frequency of play bouts			■
	Alpine marmot, *Marmota marmota*	Perrin et al. 1993	Yearling and juveniles	4 months (415 h)	-	Play behaviour			☐
	Yellow-bellied marmot, *Marmota flaviventris*	Armitage 1974	Yearlings	1714 h	-	Number of play bouts	☐		

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings		
							M > F	F > M	No sex difference
	Columbian ground squirrel, *Spermophilus columbianus*	Festa-Bianchet and King 1984	–	299 days (638 h)	-	Number of playful social interactions	■		
		Waterman 1988	Juveniles and yearlings	520 h	213	Initiations of play	□		
						Duration of play bouts	■		
		Waterman 1986	Juveniles and yearlings	–	99	Time spent in play			□
	Belding's ground squirrel, *Urocitellus beldingi*	Marks et al. 2017	Juveniles	3 months	67	Rate and duration of social play			■
	Golden hamster, *Mesocricetus auratus*	Goldman and Swanson 1975	0 to 65 days	65 days	54	Amount of playfighting	●		
	Hooded rat, *Rattus norvegicus*	Meaney and Stewart 1981	21 to 55 days	34 days	24	Play initiations	●		
Cetaceans	Bottlenose dolphin, *Tursiops truncatus*	Walker et al. 2017	< 1 year to 3 years	One year	5	Level of social play			○
Chiroptera	Common vampire bat, *Desmodus rotundus*	Park 1990	2 to 22 months	–	7	Initiations of social play	○		
Dasyuromorphia	Kowari, *Dasyuroides byrnie*	Meißner and Gansloßer 1985	0 to 220 days	220 days	43	Social play			○
Diprotodontia	Red-necked wallaby, *Macropus rufogriseus banksianus*	Watson and Croft 1993	< 20 months	2.5 years	21	Number of playfights	●		
						Median duration of playfighting bouts			●
Perissodactyla	Horse, *Equus caballus*	Rho et al. 2007	–	5 months	53	Play-fighting	■		
		Sigurjonsdottir et al. 2003	Subadults	5 weeks (488 h)	15	Dyadic play	●		
		Crowell-Davis et al. 1987	0 to 24 weeks	585 h	15	Number of play bouts	●		
						Duration of play bouts	●		
						Proportion of total play	●		

Table 2 (continued)

Order	Species	Text	Age of animals	Observation period (approximate)	Sample size	Outcome measure	Findings M > F	F > M	No sex difference
		Wells and von Goldschmidt-Rothschild 1979	–	5 months	-	Rate of play (yearlings)	■		
						Rate of play (immatures)			■
		Cameron et al. 2008	0 to 110 days	–	98	Fighting play			■
Proboscidea	African elephant, *Loxodonta* sp.	Webber 2017, Webber and Lee 2020	0 to 9 years	–	7 captive, 130 wild	Rate of play			■ ●
	Asian elephant, *Elephas maximus*	Webber 2017, Webber and Lee 2020	0 to 9 years	–	8 captive, 101 wild	Rate of play			■ ●

Circles denote captive, square denotes wild, triangle denotes wild but provisioned. Filled indicates a statistical test was carried out, blank that no test was reported

(Pérez-Barbería and Gordon 2000). All studies for this order involved captive or domestic populations.

The domestic pig, *Sus scrofa,* had three relevant texts. Dobao et al. (1985) found that sex had a significant effect on the number of observed play bouts, with male piglets participating in a greater mean number of bouts than females. Brown et al. (2018) found that sex had a significant effect on levels of social play and non-harmful fighting, with males performing significantly more social play. Brown et al. (2015) supported these findings, reporting that male piglets engaged in significantly more total social play behaviours than females. They also reported that piglets displayed sex differences in the percentages of social rather than individual play performed (41% of male piglets' play was social, compared to 31% of females' play) and that male piglets were more likely to initiate social play.

Two relevant texts were found concerning the Siberian ibex, *Capra ibex sibirica,* both concerning the same population of animals (Byers 1977, 1980). Byers (1977) reported that male ibex kids engaged in significantly more social play interactions than female kids. Byers (1980) reports that male ibex were more likely to initiate social play bouts than females, and were more likely to initiate play with related males.

Male-biased RTP was also reported for the Cuvier's gazelle (*Gazella cuvieri)*, Scimitar-horned oryx (*Oryx dammah)*, and Bighorn sheep (*Ovis canadensis)*. Gomendio (1988) reports that male Cuvier's gazelle calves engaged in significantly more play-fighting than females, although both sexes showed a similar developmental curve where RTP peaked as the individual entered the larger social group. Similarly, Hass and Jenni (1993) report that for Bighorn lambs both sexes displayed a peak of RTP at 9 to 11 weeks of age, although males consistently played at significantly higher rates. For the Scimitar-horned oryx, Pfeifer (1985) reported that significantly more bouts of social play were initiated by male calves. Neither sex displayed a significant preference for partners of the same sex, and there was no significant sex difference in the duration of social play bouts.

Three species of artiodactyla did not show a strong male bias for RTP. Sachs and Harris (1978) found that male domestic lambs (*Ovis aries*) were significantly more likely to engage in mounting and one-way butting behaviours, but there were no significant sex differences in displays of reciprocal butting. Miller (1975) also found mixed results for black-tailed deer (*Odocoileus hemionus columbianus*), with no apparent sex differences in chasing. However, playfighting was observed on 10 occasions, with only one occasion involving a female immature. For the white-lipped peccary (*Tayassu pecari*), immature females were found to engage in significantly more social play interactions than males (Nogueira et al. 2011).

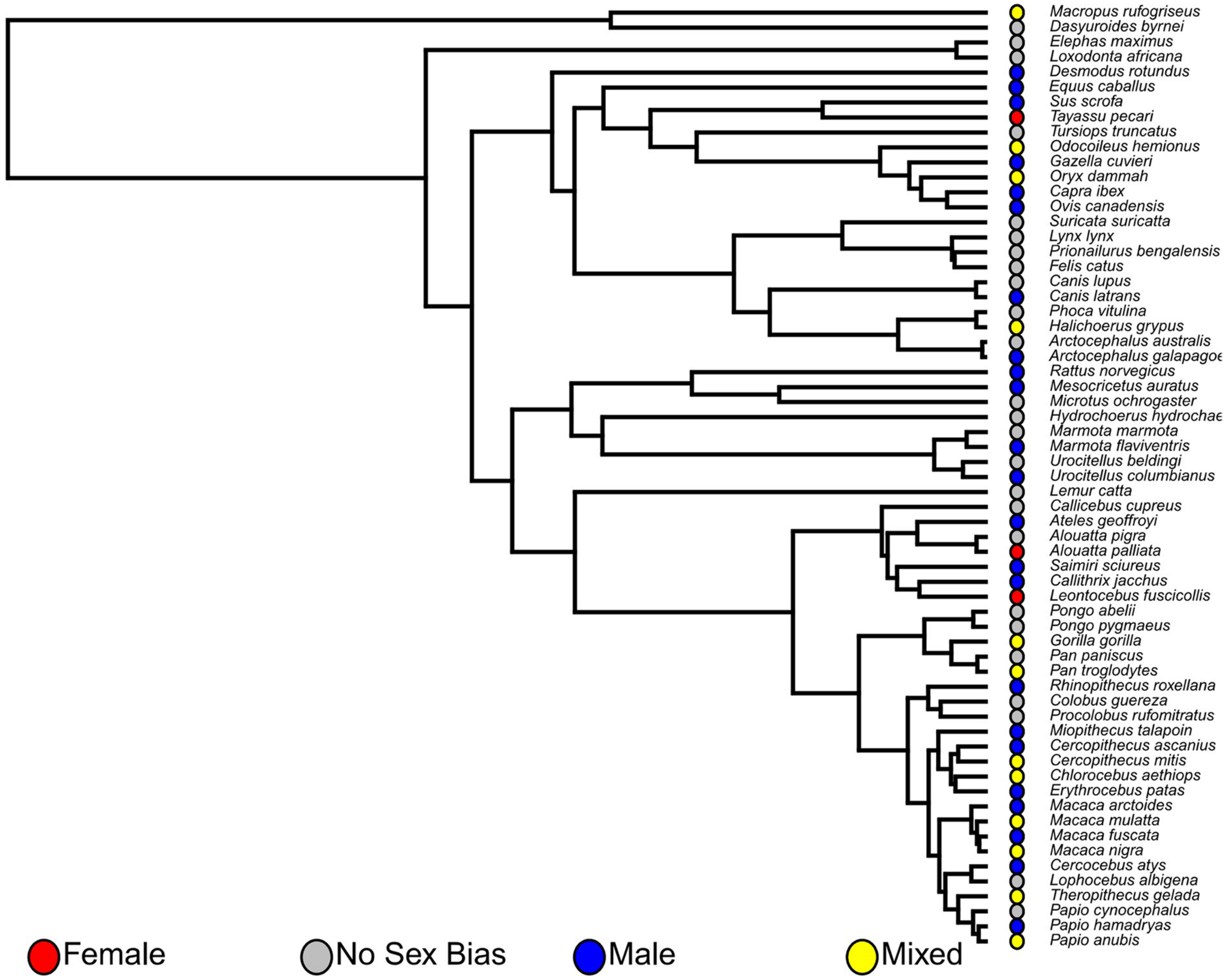

Fig. 2 Plot showing phylogenetic distribution of sex difference for RTP (rough and tumble play)

Carnivora (carnivores)

There is a large discrepancy in the energy requirements for male and female carnivorans, particularly in the breeding season, as females provide food for their young (Kidawa and Kowalczyk 2011). Male carnivorans tend to be larger, often attributed to their polygamous or promiscuous mating system (Derocher et al. 2005), which may be reflected in higher rates of RTP compared to females.

Pinnipeds, such as seals, typically display high levels of sexual size dimorphism (Lindenfors et al. 2002). Two texts contained data on grey seals (*Halichoerus grypus*), with potentially conflicting results. Cairns (2013) concluded that there were no significant sex differences between male and female pups for mean time spent in social play, although there was a trend for females to engage in more social play than males. Contradictorily, Surviliene et al. (2016) reported that subadult male grey seals were more often engaged in dyadic play bouts than females (61.76 vs 13.53%). Harcourt (1991) reports no sex differences in the play of South American fur seals (*Arctocephalus australis*) and Renouf and Lawson (1987) report no significant sex difference in the chasing behaviour of harbour seals (*Phoca vitulina*). Arnold and Trillmich (1985) report that male Galapagos fur seal pups (*Arctocephalus galapagoensis)* engage in play fighting bouts that are, on average, almost twice as long as female bouts. All studies were carried out on wild populations, but the reliability of the results is hindered by small sample sizes.

Canine species for which relevant data were found included dogs (*Canis familiaris*), coyotes (*Canis latrans*), wolves (*Canis lupus occidentalis*), bush dogs (*Speothos venaticus*), crab-eating foxes (*Cerdocyon thous*), and maned wolves (*Chrysocyon brachyurus*). For domestic dogs, male puppies initiated play more often than females,

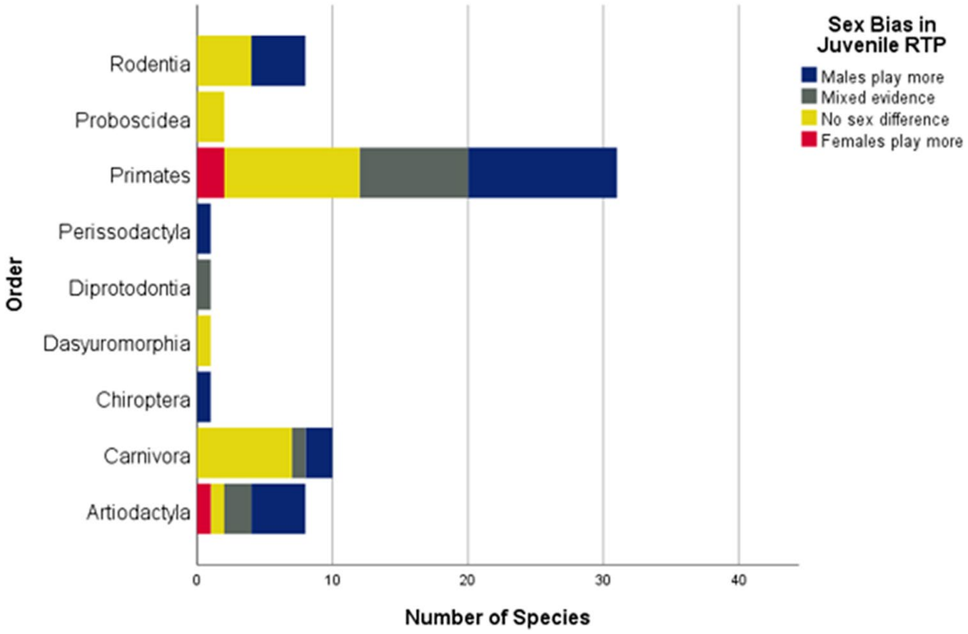

Fig. 3 Stacked bar plots showing distribution of sex biases in RTP (rough and tumble play) by order

but only significantly at weeks 7 to 8 (Lund and Vestergaard 1998), and males initiated play more often in mixed-sex dyads (Ward et al. 2008). However, for overall rates of social play, Koscinczuk et al. (2015) found no significant sex differences. For free-ranging dogs, male puppies were found to initiate RTP with a greater frequency than females (Pal 2010) and were found to engage in RTP at a higher frequency per hour than females (Pal 2008), in contrast to domestic dogs. Vincent and Bekoff (1978) reported that male coyotes showed slightly higher frequencies of play than females. For wolves, no sex differences were found for rates of RTP (Cafazzo et al. 2018), and there were no sex differences in frequency of social play behaviours for bush dogs, crab-eating foxes, or maned wolves (Biben 1983).

For the Felidae, data were found for the Eurasian lynx (*Lynx lynx*), Far-Eastern wild cat (*Prionailurus bengalensis*

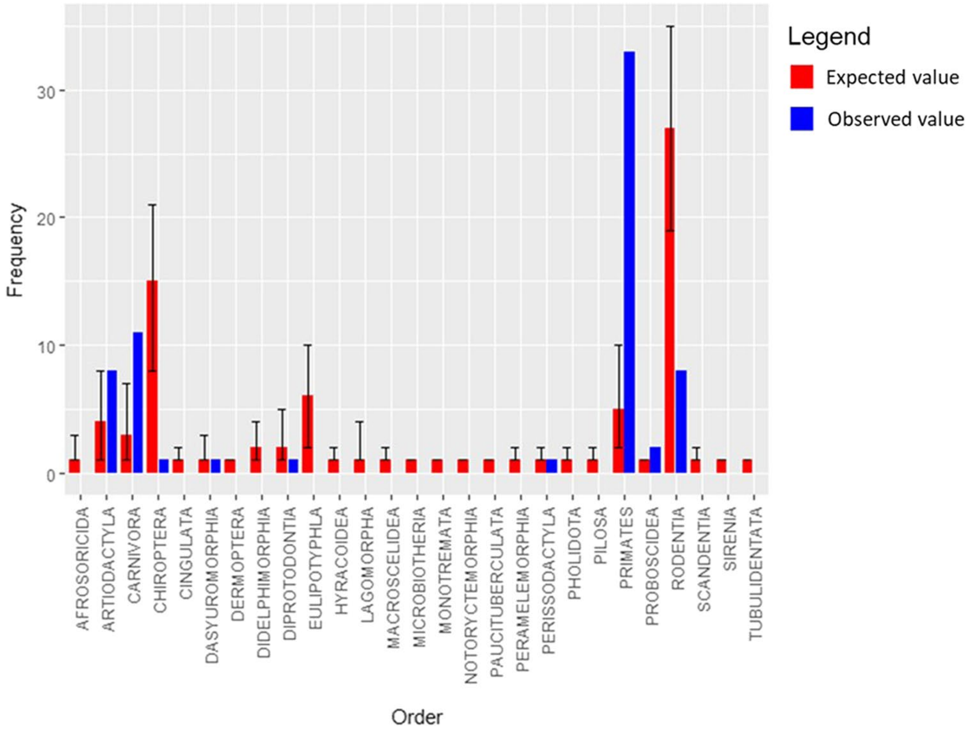

Fig. 4 Analysis of research effort, displaying expected and observed values of species included in the systematic review. Error bars represent 95% intervals

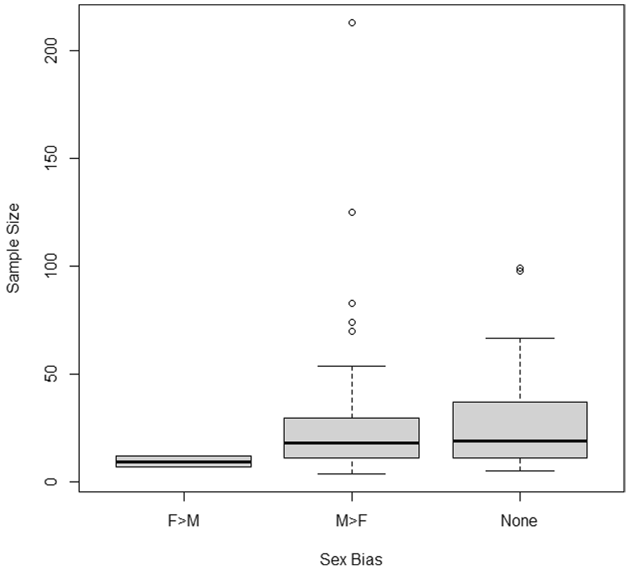

Fig. 5 Distribution of sample size between studies that found a female bias, male bias, or lack of sex bias in RTP (rough and tumble play). Boxes indicate the inter quartile range (IQR), with the central line depicting the median, the whiskers extending to 1.5*IQR, and outliers represented by circles

euplilurus), and domestic cat (*Felis catus*). Antonevich et al. (2019) report that sex did not have a significant effect on rates of social play for all three species, based on captive populations. Alekseeva et al. (2014) found no sex differences in the social play of the Eurasian lynx, and Caro (1981) found no sex differences in the social play of domestic kittens. Provisioned meerkats (*Suricata suricatta*) were also reported to display no sex differences in rates of social play (Sharpe and Cherry 2003).

Primates

Many group-living primate species are characterised by the presence of a dominance hierarchy in males and/or females, and in most primate species males disperse from the natal group (Lonsdorf 2017). Primates are unique in the length of their juvenile period relative to body size, with small litter sizes, long inter-birth intervals, extended lifespans, and high levels of investment in offspring (Joffe 1997). This long juvenile period is associated with high levels of play.

Lemuroidea (lemurs)

Data on sex differences in RTP was found for only one species of Lemuroidea, the ring-tailed lemur (*Lemur catta*), with four relevant texts. Two texts concerned the same study of a free-ranging group, in which female infants tended to engage in social play slightly more frequently than males (Gould 1989, 1990). Meredith (2018) found no significant sex difference for time spent in social play for wild ring-tailed lemurs, and Grebe et al. (2019) reported no overall sex difference in rates of play initiation but did note a significant interaction between age and sex, with females ceasing to play at earlier ages than males, in a captive group.

Atelidae

Three texts were relevant for the family Atelidae, all concerning wild populations. For the black-handed spider monkey (*Ateles geoffroyi*), males were reported to play on more occasions than females and were more likely to be involved in play bouts (McDaniel 1994). However, in a howler species of the same family, the Yucatán black howler monkey (*Alouatta pigra*), sex differences were not found in the time immatures spent playing (Rizzo 2004). Zucker and Clarke (1992) report that in the mantled howler monkey (*Alouatta palliata*), the two male infants in the study played very little compared to the older females.

Callitrichidae

Two texts were relevant for the Callitrichidae, both involving small captive groups. For the common marmoset (*Callithrix jacchus*), males were reported to play more than females (Box 1975). For the saddle-backed tamarin (*Saguinus fuscicollis*), females were reported to play more than males (Vogt 1978).

Cebidae

Five relevant texts were found for capuchins, all involving captive groups. For an unspecified species of capuchin, Fragaszy et al. (2004) report that males spent slightly more time in wrestling play, chasing, and overall social play than females. This is supported by Visalberghi and Guidi (1998), who reported that sex and age did not affect levels of engagement in play for immature tufted capuchins (*Cebus apella*). However, Paukner and Suomi (2008) found that infant male tufted capuchins spent significantly more time in wrestle and chase play than females. In the black-capped capuchin (also *Cebus apella*), male infants were reported to exhibit higher frequencies of social play behaviour compared to females (Welker et al. 1987, 1990).

Two relevant texts were selected for the squirrel monkey (*Saimiri sciureus*). Biben (1986) reported that immature males had significantly higher rates of social play and significantly longer social play bouts compared to females, in a captive group. In a later study, Biben (1989) again reported that males played at a higher rate than females.

Pitheciidae

Chau et al. (2008) reported that for captive coppery titi monkeys (*Callicebus cupreus*), sex did not have a significant effect on contact play, chasing, or pulling on tails.

Macaques

Seventeen texts had relevant data for macaques, with 7 focusing on Japanese macaques (*Macaca fuscata*). For most captive populations, immature males engaged in social play significantly more frequently than females (Eaton et al. 1985, 1986; Glick et al. 1986). Petit et al. (2008) reported that although sex did not have a significant effect on hourly frequencies of overall social play, males did wrestle more frequently and for longer durations than females. Findings for wild groups of Japanese macaques are more varied. Koyama (1986) reported that although the mean frequency of chasing and wrestling is significantly higher for males than females, the difference only becomes apparent after 4 years of age. Nakamichi (1989) reported that the median percentage of time spent in social play was higher for males than females in 10 of 17 age periods. However, Shimada and Sueur (2018) reported that for juvenile Japanese macaques, sex was not significantly correlated with the ratio of time spent in social play.

Another commonly studied macaque species was the rhesus macaque (*Macaca mulata*), with seven relevant texts. Wooddell et al. (2017) reported that male immatures initiated and participated in social play more frequently than females, Lovejoy and Wallen (1988) reported that males initiated and received rough play significantly more frequently than females, and Gard and Meier (1977) reported that males performed significantly more social and rough and tumble play than females. However, although Yanagi and Berman (2017) reported that males engaged in a significantly higher number of overall play bouts and had a higher percentage of successful play bouts (bouts which were accepted by the receiving partner leading to play) compared to females, no significant sex differences were found in the number of initiations or durations of social play bouts. Ehardt and Bernstein (1987) reported no sex differences in the amount of social play of infants, but male juveniles engaged in significantly more amounts of social play than female juveniles. Hinde and Spencer-Booth (1967) report that although males showed higher median levels of initiating RTP bouts, the sex difference was never significant. Tartabini (1991) reported that infants show no significant sex differences in initiations of play.

Data were also found for stumptail (*Macaca arctoides*) and crested (*Macaca nigra*) macaques. Bernstein (1980) reported that males played significantly more often than females, and Nieuwenhuijsen et al. (1988) reported that males had higher social play frequencies than same-aged females. For the crested macaque, sex did not have a significant effect on hourly frequencies of play, although males did wrestle more frequently and play for longer sessions than females (Petit et al. 2008).

Baboons

Six texts were found for baboons. For the Yellow baboon (*Papio cynocephalus*), Young and Hankins (1979) reported no significant sex difference in a captive group, and Cheney (1978) reported that wild male and female juveniles devoted roughly similar amounts of time to RTP. For the captive Hamadryas baboon (*Papio hamadryas*), male juveniles engaged in higher levels of dyadic play compared to female juveniles (LeResche 1976). However, all three studies of the Olive baboon (*Papio anubis*) report a significant sex difference, with provisioned males engaging in a higher median percentage of mouth-and-wrestle play (Chalmers 1980) and wild males engaging in higher levels of social and aggressive play (Owens 1975a, b).

Geladas

Three texts were relevant to geladas (*Theropithecus gelada*). Mancini and Palagi (2009) reported that captive immature males and females showed no significant difference in the frequency of contact play or the frequency of initiating play sessions. However, in a wild population, male geladas spent significantly more time in social play than females between the ages 1 and 5 (Barale 2015; Barale et al. 2015). Between 6 months and 1 year, infants engaged in similar amounts of social play, and by 6 years of age neither males nor females played enough to detect a sex difference, although female play declined faster (Barale 2015).

Vervets

Four texts were relevant to the vervet (*Cercopithecus aethiops*). Raleigh et al. (1979) reported that juvenile males engaged in RTP at a significantly higher rate than females, and Fedigan (1972) reported that males initiated higher levels of aggressive play, both for captive groups. Govindarajulu et al. (1993) reported that play frequencies did not differ by sex in a wild population. Bramblett (1978) reported that the sex differences in play change with age. Males had a higher mean rate of social play compared to females between months 1 and 47, but females had a higher mean rate of social play between months 48 and 61. Males performed the majority of their social play between 9 and 34 months.

Guenons

Guenons also showed a male bias in RTP, in both wild and captive populations. This includes the samango monkey (*Cercopithecus mitis erythrarchus*), for which males played significantly more often than females (Macleod 2000), and the talapoin (*Miopithecus talapoin*), for which males engaged in significantly more social play (Wolfheim 1977). For patas (*Erythrocebus patas*) infants, males spent more time in social play than females, with males playing in longer bouts and showing chasing behaviours more often than females (Rowell and Chism 1986). A significant male bias in RTP was found for the redtail monkey (*Cercopithecus ascanius*) when all immatures were included in the analysis (Lucci and Rothman 2020). For the blue monkey (*Cercopithecus mitis stuhlmanni*), males engaged in a significantly higher proportion of RTP, and for longer bout durations, although females engaged in a significantly higher proportion of chasing behaviour (Förster and Cords 2005).

Mangabeys

Captive male sooty mangabeys (*Cercocebus atys*) were reported to play significantly more often than females (Bernstein 1976). However, Lucci and Rothman (2020) reported no sex difference in the frequency of RTP for immature grey-cheeked mangabeys (*Lophocebus albigena*) in the wild.

Colobines

Lucci and Rothman (2020) reported no sex differences in the frequency of RTP for wild black-and-white colobus monkeys (*Colobus guereza*) or red colobus monkeys (*Procolobus rufomitratus*). Worch (2010) also reports that male and female red colobus engaged in equal amounts of RTP. However, the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) displayed a male bias in frequency of RTP (Li et al. 2011), in a provisioned group.

Gorillas

Six relevant texts concerned sex differences in RTP for gorillas (*Gorilla gorilla*), all concerning captive populations. Brown (1988) reported no sex differences in preference for the type of play, Mallavarapu (2002) reported no significant differences in time spent in social play, and Maple and Zucker (1978) reported no sex differences in engagement in RTP. However, in a study of four infant gorillas from 15 to 24 months, the male infant participated in 808 play interactions, compared to the 449, 497, and 394 play interactions of his female conspecifics (Gomez 1988). Palagi et al. (2007) reported that although there was no sex difference for gentle social play, juvenile males recorded a higher mean hourly frequency of rough social play compared to females. Hoff et al. (1981) reported a strong and consistent male bias in active social play (chasing and vigorous wrestling), but inconsistent and small sex differences in moderate social play (light bouncing and pulling).

Chimpanzees

Eleven relevant texts were selected for chimpanzees (*Pan troglodytes*). Bloomsmith et al. (1994) reported that males showed higher levels of social play than females, Nadler and Braggio (1974) reported that male immatures showed a greater proportion of RTP compared to females, and Moebius et al. (2019) reported that wild male juveniles engage in social play almost twice as much as females, and infant males engage in around 1.2 times more social play than females. Hayaki (1985) and Markus and Croft (1995) report a male bias in the frequency of RTP for captive and wild groups respectively, and Montedoro et al. (2017) report a male bias in time spent in social play for wild juveniles.

In two studies at the Arnhem zoo and TNO primate centre, Spijkerman et al. (1994, 1996) report that immature chimpanzees do show male bias in time spent in social play, although the extent of this is affected by age, component of play, setting, and peer group. In the zoo, where chimpanzees are raised in a family group, adolescent males played significantly more than females, with longer gnaw-wrestle bouts but no sex difference in chasing play (Spijkerman et al. 1994). Sex differences were not significant in other juvenile age classes, or for those raised in peer groups. Spijkerman et al. (1996) elaborate on these results, reporting that the male bias in RTP for adolescent family group chimpanzees is mainly due to longer duration of wrestling compared to females, and the increased likelihood for males to play longer than females when wrestling play was more aggressive. For younger chimpanzees, Spijkerman et al. (1996) reported a higher frequency of chasing for males, but only in the family group. The only significant sex difference for chimpanzees in both the family and peer groups was tickling, which was shown more often by females than males below 3 years of age.

In contrast, three texts suggest that there are no sex differences in social play for immature chimpanzees. De Lathouwers and Van Elsacker (2006) report no main effect of sex for time spent in social play for chimpanzee infants, and Mendoza-Granados and Sommer (1995) report that although chasing was significantly over-represented in male immatures, frequencies and durations of play bouts did not show a significant sex difference. For a wild chimpanzee group that had been provisioned in the past, Pusey (1990) reported no sex differences in rates of play.

Bonobos

De Lathouwers and Van Elsacker (2006) reported that sex did not have a significant effect on time spent in social play for captive infant bonobos (*Pan paniscus*).

Orangutans

Four relevant texts concerned various species of orangutan (*Pongo* sp.), with only one reporting a significant male bias. Nadler and Braggio (1974) reported that captive male juveniles showed a greater proportion of RTP than females, but no significant sex difference was found for chasing. However, Maple and Zucker (1978) report no sex differences in any component of RTP for another captive population of orangutans. In wild populations, both Frohlich et al. (2020) and Kunz (2015) report that sex did not have a significant effect on the occurrence of social play, for Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus wurmbii*) orangutans.

Rodentia (rodents)

Ten relevant texts contained RTP data for rodents, with most studies reporting no significant sex differences, or inconclusive results. Chau et al. (2008) reported that sex did not have a significant effect on the total play rate for captive prairie voles (*Microtus ochrogaster*) and Congdon (2007) reported no sex difference in the frequency of play bouts for wild capybaras (*Hydrochoerus hydrochaeris*). Wild alpine marmots (*Marmota marmota*) displayed no significant sex differences in RTP (Perrin et al. 1993), but wild yellow-bellied marmots (*Marmota flaviventris*) showed a trend towards higher levels of participation in play bouts for male yearlings compared to females (Armitage 1974).

Mixed results were found for ground squirrels, all of which concerned wild populations. Festa-Bianchet and King (1984) reported a significant male bias for participation in playful social interactions for two of the 3 years studied, which is supported by Waterman (1988), who reports that juvenile and yearling male Columbian ground squirrels (*Spermophilus columbianus*) initiate play more often than females and that male-male play bouts have a significantly longer duration. However, in an earlier study, Waterman (1986) reported that both sexes spent similar amounts of time in play. Marks et al. (2017) reported no significant sex differences in the rate or duration of social play for the Belding's ground squirrel (*Urocitellus beldingi*).

Mixed results were also found for captive golden hamsters (*Mesocricetus auratus*), in which immature males engaged in significantly more playfighting than expected based on the sex ratio in four of eight litters, but female-female play was lower than expected in all litters (Goldman and Swanson 1975). A significant male bias was found for captive hooded rats (*Rattus norvegicus*), for which males displayed significantly more play initiations than females for all but the first age period studied (Meaney and Stewart 1981).

Other

Cetaceans (whales and dolphins)

In a study of bottlenose dolphins (*Tursiops truncatus*), Walker et al. (2017) reported similarly low levels of social play, with no sex difference between calves.

Chiroptera (bats)

One relevant text contained data on the common vampire bat (*Desmodus rotundus*). Park (1990) reported that immature male bats seemed to initiate social play more often than females, in a captive group.

Dasyuromorphia (carnivorous marsupials)

The only relevant text for the dasyuromorphia concerned the kowari (*Dasyuroides byrnie*). Meißner and Ganslοßer (1985) report no obvious sex differences in levels of RTP for captive immature kowaris, but do comment on the difficulty of separating grooming and play behaviours.

Diprotodontia (marsupials)

Only one relevant text was found to contain data on diprotodontia, which concerned captive red-necked wallabies (*Macropus rufogriseus banksianus*). Watson and Croft (1993) reported that playfights were rare for immature female wallabies, with only three out of nine females engaging in any RTP, at a significantly lower rate than males. However, the median duration of playfighting bouts did not differ significantly between male and female wallabies.

Perissodactyla (odd-toed ungulates)

Five relevant texts were found concerning RTP in perissodactyla, all of which focused on horses (*Equus caballus*). Rho et al. (2007) reported that male Jeju pony foals were more likely to play-fight than females, although this was only recorded in relation to behaviour after mutual grooming. Sigurjonsdottir et al. (2003) report that subadult male Icelandic horses engaged in dyadic play significantly more than females, and Crowell-Davis et al. (1987) reported that male Welsh pony foals engaged in interactive play bouts significantly more often, for longer durations, and for a higher proportion of total play compared to females. Similar trends were found for the Camargue horse, for which male yearlings played significantly more often, and a similar male bias was found for younger foals, although not statistically significant (Wells and von Goldschmidt-Rothschild 1979). In feral horses, males had higher levels of involvement in fighting play than females (Cameron et al. 2008).

Proboscidea (elephants)

A PhD thesis and journal article were found containing data on RTP in elephants, although both concerned the same study. Although male calves played more than females at all ages, age and sex did not have a significant effect on overall rates of RTP for African and Asian elephants (Webber 2017; Webber and Lee 2020). However, there was a significant interaction effect between calf sex and context, as a slight male bias in RTP was more pronounced in captivity compared to wild animals.

Discussion

We confirmed that, across mammals generally, there is higher male engagement in RTP compared to females, including initiations of play and time spent in play. However, we also found an absence of sex differences in RTP across more mammalian species than expected based on prior theory and literature. For species with multiple relevant studies, mixed findings were common, which suggests sex differences in RTP are likely to vary based on context and setting. A small number of species displayed a female bias in RTP, sometimes in specific, less vigorous components of RTP, but it is difficult to conclude whether this was due to methodological factors, and important to consider that they are often not independent data points.

Potential predictors of sex differences in RTP

Sex-differentiated reproductive and life history strategies have consequences for social organisation and behaviour, which may also affect levels of sex differences in engagement in RTP. Our findings provide insight into potential predictors of engagement in RTP and help generate hypotheses to be tested.

The degree to which males are able to monopolise mating varies by species, depending on factors such as sex differences in age at maturity, ecological factors determining female dispersion, synchrony of ovarian cycles, and patterns of female cooperation in response to male mating strategies (Engelhardt et al. 2006). For most mammals, the sex that invests less in offspring care, usually males, competes more intensely for access to the opposite sex, resulting in male-male competition and formation of male dominance hierarchies, although this varies with socio-ecological factors such as the adult sex ratio of a group (Kokko and Jennions 2008). Ecological factors such as food abundance and predation risk affect components of social organisation such as group size and composition, which leads to variation in mating systems and social structures (Koenig et al. 2013), as females distribute themselves in response to resources, and males adapt to monopolise females (Emery Thompson 2017). Polygynous males are predicted to invest in body size and weaponry, which is associated with male competition, and higher levels of social play (Clutton-Brock 1988; Berghänel et al. 2015). Polygyny and promiscuity are the most common mating system of mammals, both of which predict higher levels of male competition (Kappeler et al. 2013), and therefore higher levels of RTP in males than in females in preparation for adult competition.

We found that higher levels of male RTP often coincided with higher levels of adult male aggression compared to adult females, and strict male dominance hierarchies. High dominance status for males is typically associated with greater reproductive success (Clutton-Brock 1988; Flanders et al. 2013). To the extent that RTP may function to enhance fighting skills (Cenni and Fawcett 2018), males of species with higher levels of male intrasexual competition should be more likely to engage in RTP as immatures than females. However, this pattern was somewhat disrupted by the Hominidae, for which male bias in RTP was reduced compared to predictions based on male intrasexual competition, but could be at least partly explained by small sample sizes and reliance on captive populations.

The effects of female intrasexual competition, however, must also be considered. Adult female mammals may engage in competition to secure resources including breeding sites, food sources, shelter, and mates (Stockley and Bro-Jørgensen 2011). The extent and ways in which females invest in competition are likely to vary by species. For example, the prevalence of female-female contest versus scramble competition for food depends on ecological factors (Stockley and Campbell 2013). Engagement in RTP for females is likely to change as a result of such variation, where species with high levels of intrasexual female competition which manifests as aggressive behaviour are more likely to engage in juvenile RTP.

This may be reflected in species where both sexes disperse at maturity. Dispersal is associated with increased risks of predation (Bonte et al. 2012) and a requirement of highly developed fighting and social skills (Mitani et al. 2012), which may lead to higher levels of RTP in order to develop these skills. Both the mantled howler monkey and white-lipped peccary showed a female bias in RTP (Zucker and Clarke 1992; Nogueira et al. 2011), which may be associated with dispersal in males and females for both species. Similarly, saddle-backed tamarins showed a female bias in juvenile RTP (Vogt 1978), which may have again been associated with similar levels of competition in males and females, as both male and female saddle-backed tamarins engage in infant care, although the link between paternal care and male intrasexual competition is unclear (Koenig et al. 2013). While the evidence from these species is consistent with the idea that similar levels of male and female intrasexual competition lead to reduced or female bias in RTP, the hypothesis would be difficult to test due to the small number of species that display female biased RTP.

Although in some cases a lack of sex differences might be attributed to small sample sizes and lack of statistical power, many studies with larger sample sizes reported no sex differences in either overall RTP or components of RTP. Overall, studies finding no sex differences did not have smaller sample sizes than those reporting male- or female-biased RTP. Therefore, it seems that the variation in sex biases in RTP is not simply a consequence of low statistical power.

The absence of a sex difference in play was common for the Carnivora, particularly the feliformes, suggesting that RTP may be equally important for males and females of predatory species. Carnivores are characterised by specialised diets and predatory behaviour in both males and females (Macdonald 2014), which may be developed during immature RTP (Caro 1995). In highly social carnivora, such as wolves, RTP may be used to develop social and fighting skills associated with dominance competition, as well as practice skills used in predation (Lewis 2003), which are equally necessary for males and females.

Sex differences were highly variable for primates, with many species showing mixed results or a lack of sex differences, which may have been associated with similar levels of male and female adult competition. However, equal rates of male and female play may also be due to limited sample sizes or demographics. For example, Young and Hankins (1979) only analysed the behaviour of infants below 3 months of age. Lucci and Rothman (2020) reported no significant sex differences in RTP for grey-cheeked mangabeys and red and black-and-white colobus monkeys, although again sample size was limited. They suggest that sex differences may have been observed as expected if groups were larger, as age significantly affected the choice of play partner, and often suitable partners were unavailable. The availability of play partners may have influenced the lack of sex differences found in orangutans, which have a solitary dispersed social system (Singleton and van Schaik 2002) and may have reduced opportunity to engage in RTP. Overall, it seems that a lack of sex differences in some primates seems to be associated with smaller group size and lack of suitable play partners, although low statistical power must also be considered.

Within-species variation

Webber and Lee (2020) reported higher levels of play and less time spent feeding in captive elephant calves compared to their wild counterparts, suggesting that captivity, with less constraints on energy budgets, could increase levels of RTP. However, caution must be used when comparing behaviour across environments. Differences between studies of wild and captive animals may be caused by a variety of environmental and social factors (e.g. behavioural motivation and adaptation, constraints on energy retrieval and expenditure, and welfare) and/or differences in methodology (e.g. sampling, confounding variables, and variation in ethograms and behavioural definitions) (Howell and Cheyne 2019).

Furthermore, the effects of captivity could interact with age and sex. Mixed results were found regarding sex differences in the RTP of dogs, where a male bias was more consistent in wild populations (Pal 2008, 2010) compared to captive populations where differences were only significant at certain ages (Lund and Vestergaard 1998), in specific dyads (Ward et al. 2008), or no sex difference was found at all (Koscinczuk et al. 2015). However, for Japanese macaques, the male bias in play seems to be consistent for wild and captive populations, and for chimpanzees the extent of sex differences in RTP does not seem to be dependent on whether the group was wild or captive. Therefore, the status of the group and the resulting methodology must be considered carefully for each study, as there seem to be no clear patterns of the effects of captivity with regards to sex differences in RTP.

Energetics and resource availability must also be considered as potential factors in within-species differences with respect to seasonality. Seasonal differences in levels of RTP were reported for bottlenose dolphins (Walker et al. 2017), chimpanzees (Moebius et al. 2019), and Japanese macaques (Eaton et al. 1986; Glick et al. 1986), where higher levels of play were associated with both food and play partner availability as well as hormonal changes. For chimpanzees, the effects of fruit and play partner availability were found to interact, as the effects of partner availability were significantly stronger during seasons with low-fruit availability (Moebius et al. 2019). This suggests that engagement in play can be heavily influenced by interacting factors within the social and ecological environment.

Rates and duration of RTP

Reported sex differences in RTP differ depending on the way RTP is measured, variously as rates and initiations, total time spent in play, and duration of play bouts. For example, we found that males often showed higher rates of initiation of play bouts compared to females (e.g. Siberian ibex (Byers 1980), scimitar-horned oryx (Pfeifer 1985), dogs (Lund and Vestergaard 1998; Ward et al. 2008; Pal 2010), vervet monkeys (Fedigan 1972), Columbian ground squirrels (Waterman 1988), hooded rats (Meaney and Stewart 1981) and the common vampire bat (Park 1990)), which suggests males have a higher motivation to engage in play compared to females. Dogs showed a male bias in juvenile RTP when recording initiations (Lund and Vestergaard 1998; Ward et al. 2008; Pal 2010) and frequencies (Pal 2008), but showed no sex difference in time spent in social play activity (Koscinczuk et al. 2015). Alternatively, in geladas, no sex differences were found for frequencies or initiations of RTP (Mancini and Palagi 2009), but a male bias was found for overall time spent in RTP (Barale et al. 2015). Therefore, no clear sex-biased pattern emerges, but the way that activity is recorded may influence the conclusions regarding sex differences in a species. Hence, future studies should distinguish between different measures of engagement in RTP and test hypotheses accordingly.

Components of RTP

Specific components of RTP may show different patterns in relation to sex and age. Bramblett (1978) reported that immature female vervet monkeys had a higher mean rate of social play than males, but only between 48 and 61 months old, suggesting the function of RTP may differ by sex and age. This is supported by Förster and Cords (2005), who reported that female blue monkeys engaged in a significantly higher proportion of chasing behaviour compared to males, and Spijkerman et al. (1996), who reported that females engaged in tickling behaviour significantly more often than males, but only below 3 years of age.

To understand why specific components of RTP may be valuable to males or females, the typical adult behaviours of each species must be considered. Both adult male and female vervet monkeys display high levels of aggression (Hemelrijk et al. 2020), so it is reasonable to expect that RTP will benefit both sexes in the practice of fighting skills. Immature female blue monkeys only showed higher levels of chasing play (Cheney et al. 1987), which suggests female blue monkeys are engaging in play in order to develop skills other than fighting and dominance, perhaps predator avoidance as blue monkeys are targeted by both aerial and terrestrial predators (Murphy et al. 2013). In the case of chimpanzees, grooming is important for both males and females in maintaining social bonds and establishing dominance hierarchies (Kanngiesser et al. 2011), a behaviour which may be developed in tickling play in infancy and juvenility respectively for females and males, as females mature at a slightly faster rate (Harvey and Clutton-Brock 1985).

Other considerations and future research

One major factor in the determination of sex differences in RTP which is not considered by this review is the influence of hormones on behaviour. Various endocrine studies have shown that androgenic mechanisms can influence a range of behaviours, including aggression, social dominance, and RTP (Grebe et al. 2019). Both prenatal and postnatal effects of hormones have been shown to affect engagement in RTP. For example, RTP in juvenile male rats is feminised following exposure to an androgen receptor antagonist during prenatal development (Casto et al. 2003) or increased by exposure to testosterone propionate after weaning (Pellis et al. 1992), and exposing female rats to testosterone in the womb or during postnatal development can lead to higher levels of RTP (Hines 2006). There is also some evidence that prenatal testosterone treatments can increase levels of RTP for male and female rhesus monkeys, although this is dependent on the timing and dosage of the treatment (Wallen 2005). These effects are mostly outside the scope of this review, which focuses on describing behaviour and excludes studies involving hormonal manipulations. However, the role of androgens in predisposing an animal towards RTP should be considered in further studies, as the consistency of such effects across species is not known.

The presence of a taxonomic bias in published studies towards primates, carnivores, and artiodactyla highlights a need for research into more diverse species from under-represented groups, particularly rodents which were significantly under-represented but are often involved in other types of behavioural research. However, it must be considered that play is more likely to be present in certain orders of mammal. For example, larger-brained orders, such as primates, are more likely to contain species that display play consistently (Iwaniuk et al. 2001), and this may explain some of the taxonomic bias in play research.

Despite current methodological limitations in the study of sex differences in RTP, this review helps to form a solid foundation for future comparative analyses, as it highlights potential pitfalls (e.g. taxonomic bias and methodological issues) in addition to collating and exploring the wide range of work regarding RTP and its adaptive significance in both sexes. We also identify various potential factors which may underlie variation in sex differences in RTP across mammalian species, which should be investigated further by comparative studies which take into account phylogenetic relationships between species.

Conclusions

This review summarised the extent to which a male bias in RTP was present across mammalian species, identified patterns within and between taxonomic groups, recognised potential life history-related factors that may underlie sex differences in RTP, and identified contextual and methodological factors which may have contributed to the results of the included studies. As expected, a male bias in RTP was common, particularly for initiations of play, suggesting that in many species of non-human mammal, males are motivated to play more often and for longer durations than females. Males also tended to show a preference for wrestling and more aggressive aspects of RTP, whereas females tended to show a preference for less aggressive aspects of RTP. This suggests that RTP is used as preparation for adult social behaviours, where, in many mammalian species, males engage in higher levels of aggression, and females display higher levels of social bonding. This pattern was also true to some extent where female bias in RTP was shown, with higher levels of female-female competition or lower levels of male-male competition. This pattern was also associated with a lack of sex differences in RTP, particularly for the Carnivora, which also display less divergence by sex in adult social behaviours.

Overall, we conclude that sex differences in RTP were less consistent than expected, with a large number of studies finding no sex differences in RTP. This challenges the idea that male biases in RTP are consistently more likely across juvenile mammals. Sex differences in RTP may be constrained by the environment, sample size, other methodological limitations, and taxonomic bias on reported findings, highlighting potential areas of focus for future play studies in order to support comparative research. This review generally supports the idea that engagement in RTP as an immature aids in preparation for adult roles, although strong conclusions cannot yet be drawn without statistical testing. However, there are trends in sex biases in RTP that suggest that variation in life history-related variables, such as male aggression, dominance hierarchies, and mating system may be associated with such sex differences, which should be investigated further by phylogenetic comparative analyses.

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Declarations

Ethics approval Since the research involved no primary data collection from living human or non-human participants, ethical approval was not required.

Conflict of interest The authors declare no competing interests.

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