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Play vocalisations and human laughter: a comparative review

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ABSTRACT

Complex social play is well-documented across many animals. During play, animals often use signals that facilitate beneficial interactions and reduce potential costs, such as escalation to aggression. Although greater focus has been given to visual play signals, here we demonstrate that vocalisations constitute a widespread mode of play signalling across species. Our review indicates that vocal play signals are usually inconspicuous, although loud vocalisations, which suggest a broadcast function, are present in humans and some other species. Spontaneous laughter in humans shares acoustic and functional characteristics with play vocalisations across many species, but most notably with other great apes. Play vocalisations in primates and other mammals often include sounds of panting, supporting the theory that human laughter evolved from an auditory cue of laboured breathing during play. Human social complexity allowed laughter to evolve from a play-specific vocalisation into a sophisticated pragmatic signal that interacts with a large suite of other multimodal social behaviours in both intragroup and intergroup contexts. This review provides a foundation for detailed comparative analyses of play vocalisations across diverse taxa, which can shed light on the form and function of human laughter and, in turn, help us better understand the evolution of human social interaction.

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Introduction

Play is common in a few lineages of the animal kingdom, being especially prevalent among some birds and many mammals (Burghardt 2005). Many theories of the function and types of play have been proposed, although difficulties exist, including but not limited to the basic problems of defining, identifying, and quantifying supposed play behaviour. Here we focus on social play – the most frequently described type of play in mammals. Despite its frequency, categorising this behaviour can be problematic, even in humans. The playful laughs and screams of children during wrestling, tickling, and chasing can indicate a certain non-serious mode of interaction, but the less obvious examples of social play present challenges. Consider subtle joking between adult antagonists, or verbal, emotional jousting between close social partners – identifying components that constitute play and how they relate to other social dynamics can be complex (Gibbs et al. 2014). The same can be true for

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nonhuman animals as well, compounded by challenges in identifying mental states like playfulness, and the inability to use self-report.

Smaldino et al. (2019) explored the evolutionary dynamics of play behaviour, and using a simple formal model, argued that play can evolve into different types depending on various cost/benefit tradeoffs associated with life history factors. For modelling purposes, they categorised play as either simple or complex, while acknowledging that these types likely exist on a continuum. They provided preliminary evidence that complex play – which likely enhances sociocognitive and physical motor development – requires significant investment, but can confer long-term benefits. In many cases, complex play manifests as mock fighting, and is thought to facilitate the practice and development of interactive fighting skill and calibrate defensive manoeuvring (Symons 1978; Byers and Walker 1995). An important component of this collaborative activity is that while engaged in play fighting or chasing, animals need ways to signal that their actions are neither dangerous nor done with harmful intent (Bateson 1955). Animals must also maintain fairness in order for play interaction to be evolutionarily stable (Dugatkin and Bekoff 2003; Palagi et al. 2016b). For play fighting to remain playful, species have evolved various rules of combat that, if followed, ensure that the play fighting does not escalate to aggression (Pellis and Pellis 2017). These rules managing play have co-evolved with communicative behaviours, including visual, auditory, and olfactory signals (Wilson and Kleiman 1974; Aldis 1975; Bekoff 1995; Pellis and Pellis 1996; Palagi et al. 2016a).

The most extensively studied play signals have been visual, especially the play face in primates and the play bow in canids, with vocal play signals mostly limited to reports of their occurrence and short descriptions. Here we attempt to systematise play vocalisations and develop a framework for understanding their use and evolution. We will draw explicit connections between variants of play vocalisations across nonhuman species and their corresponding socioecological contexts, with an eye towards a better understanding of the phenomenon of human laughter.

A challenge of studying play-associated vocalisations, and play signals more generally, has been the difficulty of identifying play in nonhuman animals with the usual guard against anthropomorphism. However, renewed interest in the evolution of play has led to improved methodologies for classifying it using specific behavioural conditions. For example, Burghardt (2005) proposed that for a behavioural sequence to be classified as play it must satisfy a set of five criteria. The behaviour should be non-functional in the short term, rewarding, modified from its ordinary functional form, repeated, and initiated by healthy animals in relatively unstressed contexts. In the wild, of course, categorising animal behaviours according to these criteria can be extraordinarily difficult as activity patterns are fleeting, and sequences are integrated with one another in complex (and largely unknown) ways.

There are four main categories of play described in the comparative literature: locomotor, object, social, and fantasy play (Pellegrini and Smith 2005). Rough-and-tumble play, sometimes referred to as play fighting, is a subcategory of social play marked by wrestling, chasing, and gentle biting (Aldis 1975). Play fighting is widespread across mammals and especially predominant in primates. Importantly, it constitutes the category of play most associated with vocalisations (Bekoff and Allen 1998). The vocal channel is effective for signalling during play fighting because the partner's face may

not always be visible. Rapid detectability is a crucial dimension in play signalling, and evidence suggests that visual signals, such as play bows in dogs (*Canis lupus familiaris*), occur at junctures in the play action that maximises their salience (e.g., during moments of physical separation with face-to-face positioning; Cordoni et al. 2016). Vocal signals do not require special positioning to work, but still might be produced systematically in an attempt to optimise their effectiveness (e.g., with specific temporal relationships to upcoming behaviour).

The study of vocal signalling during play presents researchers with a classic problem, illustrative of not only more general problems concerning the meaning of animal signals (Rendall et al. 2009; Fischer and Price 2017), but also the issue of redundancy (Wiley 2006). Vocal play signals frequently accompany other non-vocal behaviours, such as the play face in primates (Van Hooff 1972) or the play bow in dogs (Bekoff 1995). Play vocalisations may reinforce or emphasise the non-vocal signals, or add specific information not contained in other behaviours. Moreover, vocalisations that are common during play often occur additionally in non-playful interactions (Pellis and Pellis 1996). Thus, it becomes difficult to determine exactly how vocal signals are functioning across varying contexts, especially when the vocalisations are acoustically similar across them. Many constraints shape the evolution of context-specific signalling across taxa (Townsend and Manser 2013). Some species might have one or more play-specific signals, while others use more general signalling behaviours in context-sensitive ways. A comparative analysis focusing on form and function relationships between signal characteristics and behavioural strategies allows theorists to evaluate how signals operate in context, as well as understand their phylogenetic history through identifying common ancestry (homology) or independent but convergent adaptations (homoplasy).

In evolutionary biology, structural characteristics of traits (i.e., their forms) can be understood with reference to their observed functions. This theoretical framework has proven invaluable across different areas of study including functional morphology, behavioural biology, and signal design. The idea applies to play in at least two ways. Behavioural analyses of play reveal clear connections between the recurrent action patterns of animals engaged in play and the ultimate functional benefits of those actions. For example, play fighting has characteristics that facilitate the development and calibration of adult fighting skills, such as nonaggressive fight simulation and turn-taking in role-play (i.e., being attacker versus victim). In the case of vocal signalling, acoustic features of vocalisations are inherently connected to their communicative functions, such as loud and noisy features of alarm calls that grab receivers' attention (Owren and Rendall 2001; Blumstein and Récapet 2009). Form and function logic has informed efforts to understand human vocal signalling as well (Bryant 2020b). For example, in infant-directed speech, loud and abrupt acoustic features of prohibitives (e.g., 'No!') can function to redirect an infant's attention and interrupt undesired behaviour. Conversely, slow rising pitch intonations and lilting speech rhythms can encourage other behaviours (Fernald 1992; Bryant and Barrett 2007). The aversive sound qualities of infant crying are easily understood as shaped by selection to cause behaviour in caretakers that results in crying cessation (Soltis 2004), and these features extend to distress calls in nonhuman species as well, indicating conserved structure (Lingle et al. 2012). As we describe below, the form–function approach can help us understand the communicative functions of play vocalisations, including human laughter.

Play vocalisations across species

We conducted an exhaustive literature review searching empirical reports that included descriptions of play vocalisations in any animal species. Our aim in this summary of the literature is not necessarily to identify every paper reporting such behaviour, but instead compile a reasonably complete survey of the animal behaviour literature to date in order to establish any pattern of structural features that can be plausibly linked to human play vocalisations, typically manifesting as laughter. Many of these descriptions appear in studies that focused on other aspects of animal social behaviour, and most only provide verbal descriptors of the vocal sound. We found reports of vocal play signals throughout the mammal literature, especially among primates, rodents, social carnivores, and (to a lesser extent) marine mammals. In the case of primates, play vocalisations are documented in the majority of species that have been studied extensively. Additionally, researchers have described at least three species of birds with play-specific calls.

Table 1 presents the list of species ($N = 65$) for which we found reports of play vocalisations, and we include information (if available) regarding whether there is evidence that the vocalisation is specific to play contexts, as well as verbal descriptors of the sound particularly concerning: a) noisy (i.e., broadband energy) versus tonal (harmonic structure), b) loud versus quiet, c) high versus low pitch, d) short versus long duration, and e) single calls versus regularity (i.e., rhythmic series).

While all of the vocal behaviours listed in Table 1 are explicitly described as having occurred during play interactions, some were described both in play and other behavioural contexts. Thus, ‘play-specific’ indicates vocalisations described as occurring *only* during play and not in any other context. Further research may reveal that some signals are characteristic of social play, but still manifest infrequently in other contexts – perhaps marking a playful mood outside of recognisable social play interactions. Alternatively, the vocalisations may have multiple subtypes, only some of which occur during play. For example, detailed analysis of dog growls reveals that playful growls have a different acoustic signature from aggressive growls; as such, labelling these two subtypes as ‘growl’ could misleadingly suggest non-specificity of the call context (Faragó et al. 2010). Additionally, many studies briefly mention vocalisations associated with play, without sufficient detail for determining whether they exclusively occur during play. Fagen’s (1981) description of play in margays (*Leopardus wiedii*) is typical:

‘... their play is usually quiet as well, but there are exceptions to this rule. Vocalizations have the effect of controlling play, and it is always possible for an observer to detect that a margay play-bout is becoming rough when the animals begin making a low growling or rough purring sound whose intensity may rise if roughness continues’ (p. 173).

That these vocalisations increase with play intensity and ‘control’ play suggests that they provide specific facilitative functions within play, similar to the laughter-like play vocalisations in the great apes. But the margay vocalisations could simply indicate pain or aggression that happens to occur in the course of rough play, rather than being play-specific. A more complete understanding of the functional significance of vocalisations during play interactions is needed in order to determine the phylogenetic relationship of these signals across extant species.

Table 1. List of species for which we found reports of play vocalisations.

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Great apes	Human	<i>Homo sapiens</i>	Bachowski et al. (2001)	No	Laughter	Loud or quiet, tonal and noisy, high and low frequency, short, rhythmic and single
Great apes	Chimpanzee	<i>Pan troglodytes</i>	Van Lawick-Goodall (1968); Marler and Tenaza (1977); Van Hooff and Preuschoft (2003); Matsusaka (2004)	Yes	'staccato, throaty panting,' laughter	Quiet, tonal and noisy, short, low frequency, rhythmic
Great apes	Bonobo	<i>Pan paniscus</i>	de Waal (1988); Förderreuther and Zimmermann (2003)	Yes	Panting laugh; laughter	Quiet, noisy, low frequency, short, rhythmic (irregular)
Great apes	Western lowland gorilla	<i>Gorilla gorilla gorilla</i>	Salmi et al. (2013)	Yes	Panting chuckle	Quiet, low frequency, short, rhythmic
Great apes	Mountain gorilla	<i>Gorilla beringei beringei</i>	Schaller (1963); Fossey (1972)	Yes	Panting chuckle (a-a-a-a)	Quiet, noisy, low frequency, short, rhythmic
Great apes	Sumatran orangutan	<i>Pongo abelii</i>	Rijksen (1978)	Yes	'ahh,' play-grunt, laughter	Quiet, low frequency, short, rhythmic
Great apes	Bornean orangutan	<i>Pongo pygmaeus</i>	Chevalier-Skolnikoff (1982), Davila Ross (2007)	Yes	Laughter	Quiet, low frequency, short, rhythmic
Lesser apes	White-handed gibbon	<i>Hylobates lar</i>	Davila Ross (2007)	Unclear	Low frequency vocalisations	Low frequency
Lesser apes	Siamang	<i>Symphalangus syndactylus</i>	Davila Ross (2007)	Unclear	Low frequency vocalisations	Low frequency
Old world monkeys	Olive baboon	<i>Papio anubis</i>	Smuts (1985); Lewis (2005)	Yes	Voiceless chuckles; play chuckle	Quiet, noisy
Old world monkeys	Hamadryas baboon	<i>Papio hamadryas</i>	Kummer and Kurt (1965); Aldis (1975); Leresche (1976)	Yes	Coughs	Quiet, noisy, low frequency, short, rhythmic
Old world monkeys	Vervet monkey	<i>Chlorocebus aethiops</i>	Struhsaker (1967); Fedigan (1972); Masataka and Kohda (1988)	Yes	Panting; purr	Quiet, low frequency
Old world monkeys	Patas monkey	<i>Erythrocebus patas</i>	Hall (1965)	Unclear	Nickering	Quiet
Old world monkeys	Barbary macaque	<i>Macaca sylvanus</i>	Preuschoft (1992); Kipper and Todt (2002); Vettin and Todt (2005)	Yes	Low intensity voiced breathing; chuckle	Quiet, noisy, rhythmic
Old world monkeys	Rhesus macaque	<i>Macaca mulatta</i>	Symons (1978)	Yes	Panting	Quiet, noisy
Old world monkeys	Moor macaque	<i>Macaca maura</i>	Aldis (1975)	Unclear	Chattering	Quiet
Old world monkeys	Japanese macaque	<i>Macaca fuscata</i>	Itani (1965) as described in Goedeke and Immelmann (1986)	Unclear	N/A	N/A

(Continued)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Old world monkeys	Northern plains grey langur/Hanuman langur	<i>Semnopithecus entellus</i>	Sugiyama (1965)	Unclear	Heavy breathing	Quiet, noisy
Old world monkeys	King colobus	<i>Colobus polykomos</i>	Kirschhofer (1960) as described in Aldis (1975)	Yes	Smacking	N/A
Old World Monkeys	Silver leaf monkey/Silver lutung	<i>Trachypithecus cristatus</i>	Masataka and Kohda (1988)	yes	peep-like or squeal-like	tonal, high frequency
Old World Monkeys	François' leaf monkey/François' langur	<i>Trachypithecus francoisi</i>	Masataka and Kohda (1988)	Yes	Peep-like or squeal-like	Tonal, high frequency
Old World Monkeys	John's leaf monkey/Nilgiri langur	<i>Trachypithecus johnii</i>	Poirier (1970)	Unclear	Peep-like or squeal-like	Tonal, high frequency
New world monkeys	Golden-backed uakari	<i>Cacajao</i>	Bezerra et al. (2010)	Yes [reco]	Reco call, áhh call	Reco: short, single or series áhh: quiet, noisy, short, single
New world monkeys	Geoffroy's spider monkey	<i>melanocephalus Ateles geoffroyi</i>	Aldis (1975)	Unclear	Chattering	Quiet, noisy, rhythmic
New world monkeys	Mantled howler	<i>Alouatta palliata</i>	Baldwin and Baldwin (1976)	Unclear	Whimpers	Tonal, high frequency
New world monkeys	Common squirrel monkey	<i>Saimiri sciureus</i>	Winter et al. (1966); Baldwin and Baldwin (1974); Biben and Symmes (1986); Masataka and Kohda (1988)	Yes	Cackles, peeps	Cackles: N/A peeps: high and increasing frequency
New world monkeys	Goeldi's monkey	<i>Callimico goeldii</i>	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Golden lion tamarin	<i>Leontopithecus rosalia</i>	McLanahan and Green (1977); de Oliveira et al. (2003)	Unclear	Rasp, trill, peep, chatter, squeal	Varies
New world monkeys	Saddleback tamarin	<i>Leontocebus fuscicollis</i>	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Common marmoset	<i>Callithrix jacchus</i>	Stevenson and Poole (1982); Masataka and Kohda (1988)	Yes	Whirr/peee, tsak/tsik, ngá	Varies
New world monkeys	White-lipped tamarin	<i>Saguinus labiatus</i>	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Cotton-top tamarin	<i>Saguinus oedipus</i>	Cleveland and Snowdon (1982); Goedecking and Immelmann (1986); Goedecking (1988)	Unclear	Whistles, squeals	Varies; unstable frequency
Strepsirrhines	Senegal bushbaby	<i>Galago senegalensis</i>	Zimmermann (1989a)	Unclear	Week, week, wak	Tonal

(Continued)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Strepsirrhines	Slow loris	<i>Nycticebus coucang</i>	Zimmermann (1985); Zimmermann (1989b)	Unclear	Call type II.4, chro	Call type II.4: quiet, noisy and tonal, short, series chro: high frequency, short
Strepsirrhines	Ring-tailed lemur	<i>Lemur catta</i>	Macedonia (1993)	Unclear	Trills, hmms	Quiet
Strepsirrhines	Gray mouse lemur	<i>Microcebus murinus</i>	Zimmermann (1991); Scheumann et al. (2007)	Unclear	Trill, tsak	N/A
Rodents	Laboratory rat	<i>Rattus norvegicus</i>	Knutson et al. (1998); Burke et al. (2017a)	Yes	50 kHz calls with several subtypes	Short, high frequency, rhythmic
Rodents	Degu	<i>Octodon degus</i>	Wilson and Kleiman (1974); Long (2007)	Unclear	Purring/gurgling, warble	Purring/gurgling: quiet, long warble: quiet, high frequency, short, single
Rodents	Mongolian gerbil	<i>Meriones unguiculatus</i>	Holman and Seale (1991)	No	Ultrasonic vocalisations	High frequency
Carnivores (Canids)	Domestic dog	<i>Canis lupus familiaris</i>	Bekoff (1974); Bekoff (1995); Feddersen-Petersen (2000); Robbins and McCreery (2003); Simonet et al. (2005); Faragó et al. (2010)	Yes	Bark, panting, growl, yelp	barks: loud, tonal growls: quiet, noisy, variable duration, low frequency, series, panting: quiet, noisy, rhythmic
Carnivores (Canids)	Red fox	<i>Vulpes vulpes</i>	Cohen and Fox (1976)	Unclear	Panting	yelp: loud, tonal, high frequency
Carnivores (Canids)	Bat-eared fox	<i>Otocyon megalotis</i>	Lamprecht (1979)	No	Snarl	Quiet, noisy, rhythmic
Carnivores	European badger	<i>Meles meles</i>	Eibl-Eibesfeldt (1950) as described in Goedeking and Immelmann (1986)	Unclear	N/A	High frequency
Carnivores (Mustela)	Louisiana mink	<i>Neovison vison</i>	Svihla (1931)	Unclear	Hissing, squealing, growling	N/A
Carnivores (Mustela)	European polecat	<i>Mustela putorius</i>	Poole (1966)	Unclear	Clucking, hissing	Varies
Carnivores (Mustela)	Ferret/Domesticated polecat	<i>Mustela putorius furo</i>	Goethe (1940); Fagen (1981)	Unclear	Chattering, Klaffen	Quiet
Carnivores (Mustela)	Stoat/ermine	<i>Mustela erminea</i>	Fagen (1981)	Unclear	Mucker, grumble softly, purr, mutter	Quiet, noisy, rhythmic
Carnivores (Mustela)						Quiet, low frequency

(Continued)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Carnivores (Pinnipeds)	California sea lion	<i>Zalophus californianus</i>	Schusterman et al. (1966); Peterson and Bartholomew (1967); Peterson and Bartholomew (1969); Aldis (1975)	No	Barks, clicks, whinnies, bleats, unvoiced or voiced cough	Loud, short
Carnivores (Pinnipeds)	Harbour seal/Common seal	<i>Phoca vitulina</i>	Wilson (1974)	Unclear	Woah	Loud
Carnivores	American black bear	<i>Ursus americanus</i>	Henry and Herrero (1974)	Unclear	Panting and breathing sounds	Quiet, noisy, rhythmic
Carnivores	Egyptian mongoose	<i>Herpestes ichneumon</i>	Rensch and Dückler (1959) as described in Goedecking and Immelmann (1986)	Unclear	N/A	N/A
Carnivores	Indian grey mongoose	<i>Urva edwardsii</i>	Rensch and Dückler (1959) as described in Goedecking and Immelmann (1986)	Unclear	N/A	N/A
Carnivores	Common dwarf mongoose	<i>Helogale parvula</i>	Rasa (1984)	Yes	Pulse	Short, high frequency, series
Carnivores (Cats)	Margay	<i>Leopardus wiedii</i>	Petersen (1979); Fagen (1981)	Unclear	Low growling/purring, harsh miaows and growls	Quiet, noisy, low frequency
Carnivores (Cats)	Pallas's cat	<i>Otocolobus manul</i>	Fagen (1981)	No	Hiss	Quiet, noisy
Carnivores (Cats)	Domestic cat	<i>Felis catus</i>	Fagen (1981)	No	Hiss	Quiet, noisy
Carnivores (Cats)	European wildcat	<i>Felis silvestris</i>	Fagen (1981)	No	Hiss	Quiet, noisy
Cetaceans	Bottlenose dolphin	<i>Tursiops truncatus</i>	Herzing (1996); Blomqvist et al. (2005)	Yes	Pulse burst, whistle, squawk	Varies
Cetaceans	Atlantic spotted dolphin	<i>Stenella frontalis</i>	Dudzinski (1998)	Unclear	Whistle	Tonal
Cetaceans	Killer whale	<i>Orcinus orca</i>	Rehn et al. (2007)	Unclear	V4 type calls, 'chatter'	Modulated frequency, series
Ungulates	Rocky Mountain elk	<i>Cervus canadensis nelsoni</i>	Altmann (1958)	Unclear	Squeal	High frequency
Ungulates	Domestic cow	<i>Bos taurus</i>	Schloeth (1961) as described in Bouissou et al. (2001)	Yes	N/A	N/A
Proboscids	African elephant	<i>Loxodonta africana</i>	Langbauer (2000); Poole (2011)	Yes	Nasal trumpet	Loud, tonal
Marsupials	Eastern grey kangaroo	<i>Macropus giganteus</i>	Watson (1998)	Unclear	Cough	Quiet, low frequency, short

(Continued)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Birds (Parrots)	Kea parrot	<i>Nestor notabilis</i>	Schwing et al. (2017)	Yes	Warble	Loud
Birds (Parrots)	Budgerigar	<i>Melopsittacus undulatus</i>	Diamond and Bond (2003)	Unclear	Soft croaking	Quiet, low frequency
Birds	Australian magpie	<i>Gymnorhina tibicen</i>	Pellis (1981)	Yes	Guttural sounding call	Quiet, low frequency, long

*This column indicates acoustic descriptors based on available reports in the literature. Acoustic dimensions include loudness (loud/quiet), harmonicity (tonal/noisy), frequency (low/high), call duration (short/long), and repetition (single, rhythmic, or series). N/A indicates a missing or ambiguous description.

Evidence for play vocalisations in non-mammal vertebrates (e.g., birds, reptiles, and fish) is extremely limited. Play is particularly difficult to identify in non-mammals, but some researchers have argued for its presence in birds and potentially even some reptiles (e.g., turtle object play) and fish, although this should be viewed as preliminary (Burghardt 2005). To our knowledge, two bird species in the parrot group and Australian magpies (*Gymnorhina tibicen*) are currently the only non-mammals that have been clearly described using distinct vocalisations during social play (Pellis 1981; Diamond and Bond 2003; Schwing et al. 2017). [Figure 1](#) shows a cladogram displaying the phylogenetic relationship between all species currently known to produce play vocalisations, based on NCBI taxonomy (Letunic and Bork 2007; Letunic 2020).

Vocal systems are subject to a number of constraints (e.g., predation risk, anatomical factors, sexual selection, etc.) that might have decoupled vocalisations from play in some species. Whether play behaviour itself is homologous across mammals, and possibly even across vertebrates, is yet to be determined (Burghardt and Pellis 2019). One possibility is that the underlying (and sometimes latent) biological machinery proximately motivating play (such as an endogenous reward system triggered by positive social interaction) is homologous across mammals, but differences in play vocalisations arise from variation in the vocal repertoire and cost/benefit tradeoffs of play signalling across different species. Consequently, in a given comparison between two species with similar play behaviours, we might find homology in the physical play sequence, but homoplasy in the associated signalling, or in the specific attributes of that signalling. Indeed, research on play in rats (discussed in detail below) is suggestive of this pattern. To answer these evolutionary questions, we need better comparative data on the variation in acoustic features of play vocalisations, and the ways that specific features covary with ecology and phylogenetic relatedness.

Acoustic features of play vocalisations

Many scholars have noted the similar forms of play vocalisations across the great apes, identifying them as variants of laughter (Darwin 1872; Van Hooff 1972; Provine 2000). Vettin and Todt (2005) examined play vocalisations in Barbary macaques (*Macaca sylvanus*), chimpanzees (*Pan troglodytes*), and adult humans, all occurring during tickling episodes, and found that in humans and chimpanzees, there was similar high intrabout variability in call interval duration and fundamental frequency – auditory features that seem to play an important role in making a vocalisation sound like a laugh (Kipper and Todt 2001). All species produced serially organised calls, and interval durations between expiratory and inspiratory elements were similar. However, macaque calls tended to lack harmonic structure and were significantly lower in amplitude.

Acoustic characteristics of play vocalisations can provide insight into their evolutionary history. Davila Ross, Owren, and Zimmermann (2009) reconstructed the phylogeny of great ape play vocalisations through acoustic analysis and suggested that all ape ‘laughter’ can be traced to the play vocalisation of a common ancestor that lived approximately 18 MYA. The evolutionary trajectory leading to current ape species appears to have shifted towards vocalisations with increased vibration regimes (i.e., greater voicing/more tonal), shorter bursts, and longer bouts. Airflow is also universally

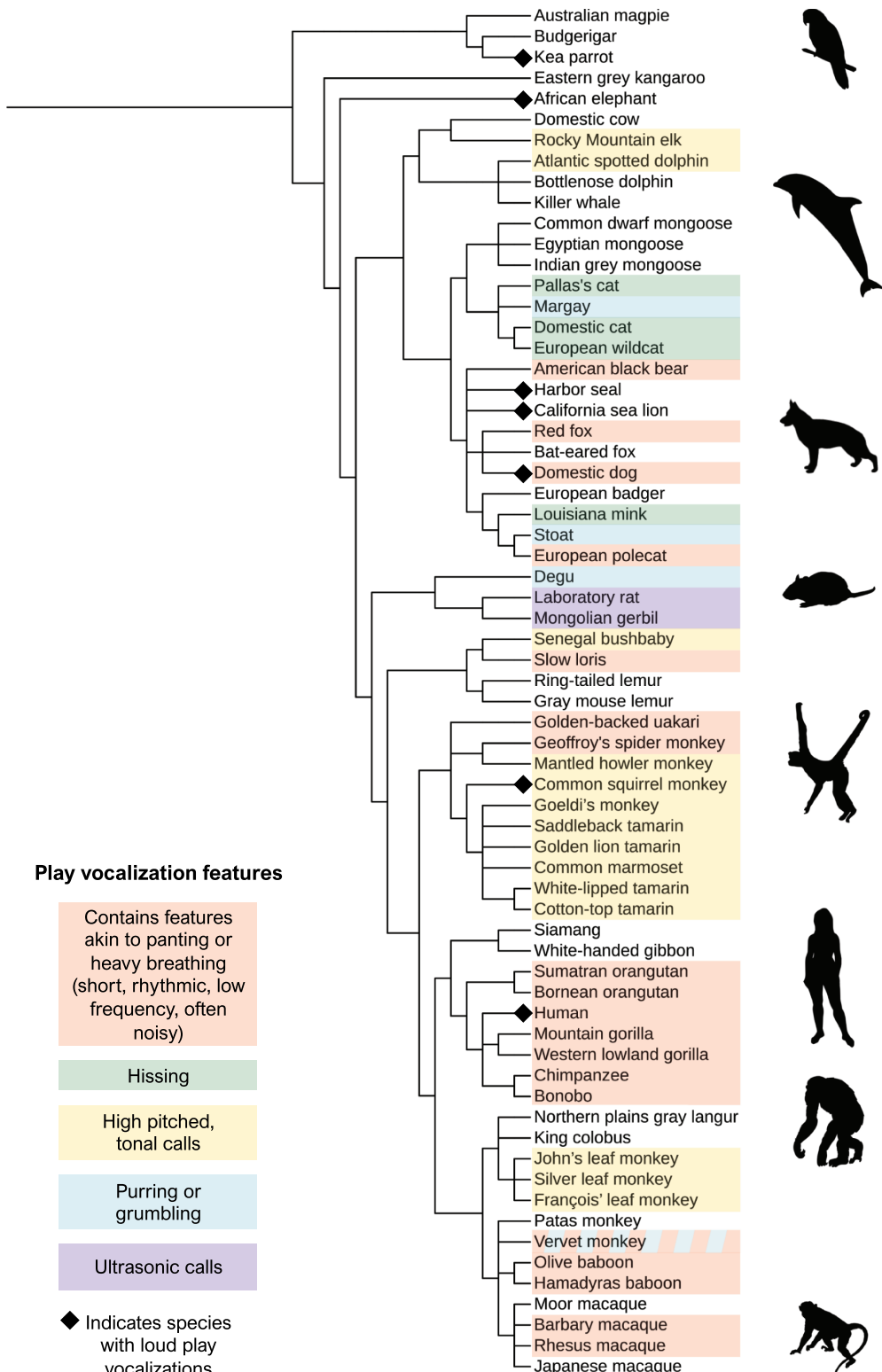


Figure 1. Cladogram illustrating the phylogenetic relationship between all species reported to have play vocalisations, including designations of vocal features across clades.

aggressive, with the exception of chimpanzees who more typically produce laughter calls with alternating airflow.

Existing research has uncovered acoustic similarities across primate species, but few other comparative studies have been conducted. Our extensive literature review, comprised of a variety of mammals and a few birds, reveals a general trend: play vocalisations are most commonly described as short, serially organised, low amplitude bursts. While these commonalities are notable, there is still significant acoustic variation across species. Play vocalisations range from quiet hissing to harmonic barks, including tonal squeals, low-pitched grunts, noisy chattering, and ultrasonic trills. [Figure 2](#) shows representative spectrograms of play vocalisations in different taxa as an example of this variation. Still, even in these different forms, play signals are usually quiet. The inconspicuous nature of the signals is generally attributed to predator avoidance – loud broadcasts of play behaviour can attract predators, and a quiet signal will suffice if the signallers are in close proximity to one another. Loud signals, such as human laughter, are exceptions to the rule, and we describe implications of this below.

Despite the profoundly incomplete record of play-associated vocal behaviour across animals, as well as inconsistent reports of sound features in those that have been described, some lineages exhibit clearly divergent acoustic patterns. For example, in Old World monkeys, two subfamilies appear to have distinct vocal behaviours. In the subfamily *Cercopithecinae*, such as baboons and macaques, play vocalisations tend to be quiet, noisy, and rhythmic. But in close relatives from the subfamily *Colobinae*, such as several leaf monkey species, play vocalisations tend to be tonal, high-pitched peeps and squeals. New World monkeys, such as squirrel monkeys, howler monkeys, and spider monkeys, also often produce tonal, high-pitched peeps and chatters. As mentioned earlier, great ape play vocalisations share many properties with human laughter, and are usually described as panting or chuckling.

Indeed, many of the play vocalisations mentioned in [Table 1](#), particularly among primates and carnivores, are described as ‘panting,’ or some form of laboured breathing. These pants are voiced in some species and unvoiced in others. Other types of play vocal signals have acoustic features similar to panting, in that they are described as rhythmic, staccato, chuckling, or chattering. These qualities are consistent with the notion that play vocalisations evolved from heavy breathing during play. Because rough-and-tumble play requires a high level of physical exertion, unvoiced rapid or heavy breathing during play likely originated as an acoustic cue of energy expenditure and investment in the play activity (Provine 2000). Through a ritualisation process (Tinbergen 1952), the vocal pattern was then shaped into a communicative signal of benign intent that clarified mutual positive investment in the activity and induced positive affect, which helped prolong the play. This process potentially occurred in a mammalian common ancestor, meaning that all current mammalian play vocalisations are homologous. By this perspective, any variation in the acoustic features of play vocalisations across mammals evolved from an ancestral pant-like sound via species-specific vocal evolution. Convergence in similar, atypical acoustic traits across disparate species could constitute homoplasy (e.g., loud barking vocalisations in both sea lions and dogs), even if the underlying behavioural adaptation of producing play vocal signals is homologous. Alternatively, convergent evolutionary dynamics might have afforded the independent evolution of play vocalisations multiple times over mammalian evolutionary history.

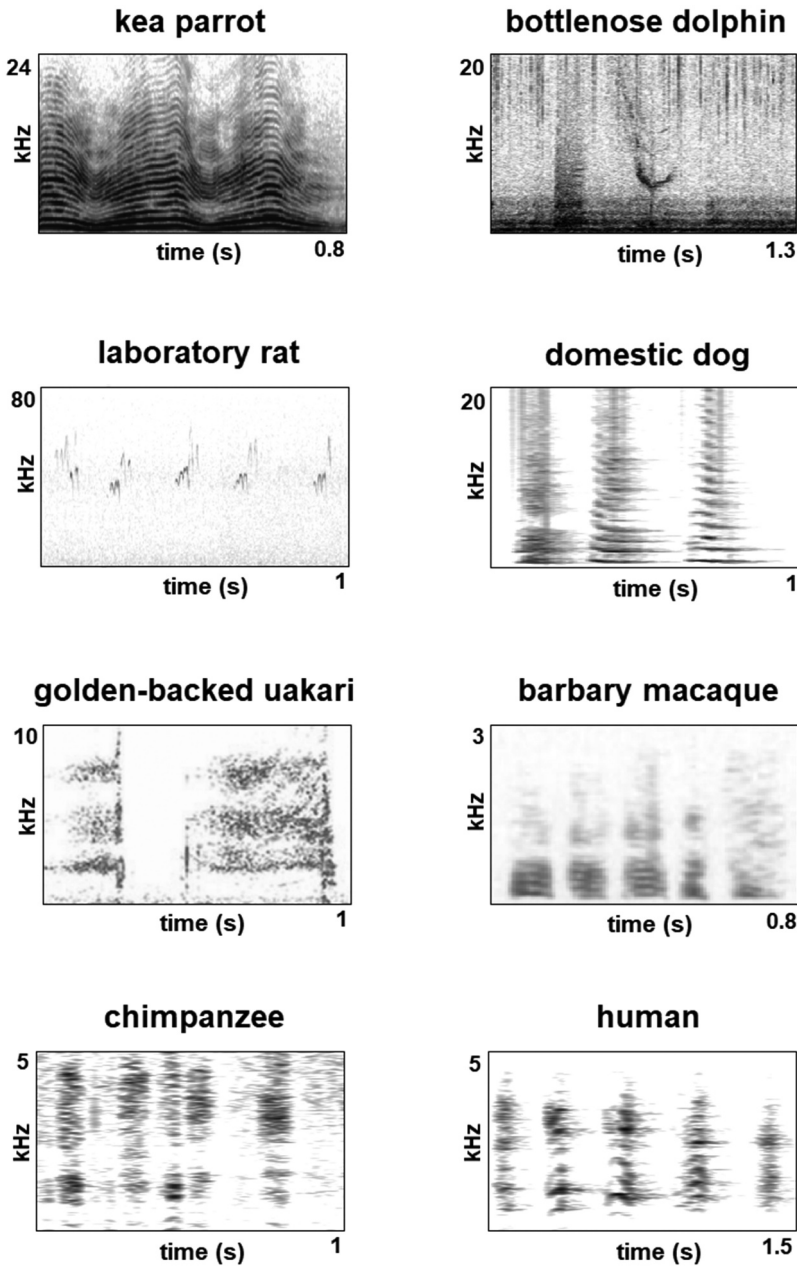


Figure 2. Spectrogram examples of play vocalisations across disparate species.

Vocal signals of play in rats (*Rattus norvegicus*) illustrate this phylogenetic puzzle nicely. Knutson et al. (1998) first documented ultrasonic vocalisations (USVs ~50 kHz) emitted by juvenile rats during play, and in a series of experiments, demonstrated that they were associated with positive affect. An earlier account associated similar vocalisations with chasing and sexual activity (Sales 1972). Since then, a fair amount of evidence

has accumulated revealing that many vocalisations comprise the category of USVs and distinct subtypes are reliably associated with specific behaviours in the sender, and responses in receivers (for a review, see Burke et al. 2020). Interestingly, some USVs are potentially tied to breathing. Burke et al. (2017b) described the *movement byproduct hypothesis* – an attempt to explain vocalisations as artefacts of particular jumping and exertion during high activity. As Burke et al. pointed out, this cannot explain the current vocal behaviour, but it could plausibly account for antecedent vocal cues that became ritualised, as described earlier. This presents a good case for convergent evolution in that USVs associated with play evolved in the context of a larger repertoire in rodent species (see also Sangiamo et al. 2020), but independently from primates that also have evolved play-associated vocal signalling. It is additionally worth noting that tickling of rats by human experimenters evokes these 50 kHz signals (Panksepp and Burgdorf 2000), which could point to deep homologies in the underlying neurological mechanisms, despite differences in the acoustic features of the calls and their evolutionary history.

While rat USVs clearly represent a unique form of mammalian play vocalisations, there are other acoustic distinctions across species' play vocalisations that suggest theoretical alternatives to being evolved from laboured breathing. For example, among several New World primates (*Platyrrhini*), play vocalisations are often described as high-pitched peeps, whistles, or squeals (Cleveland and Snowdon 1982; Biben and Symmes 1986; Masataka and Kohda 1988). Masataka and Kohda (1988) argued that these vocalisations evolved from a location or contact call given by infants towards their mothers during allomothering, rather than from laboured breathing during play. In these species, evolutionary convergence could explain the independent evolution of play vocalisations derived from a unique, pre-existing vocal repertoire.

Other types of play vocalisations are more difficult to interpret. For example, 'nasal trumpets' given by elephants (*Loxodonta africana*) during play could plausibly be derived from a type of heavy breathing, as elephants expel bursts of air through their trunks during physical exertion (Soltis 2010; Poole 2011). However, the clicks, pulses, and whistles produced by marine mammals during play are unlikely to be intimately tied to breathing, due to the evolutionary constraints on marine mammals' breathing and vocal apparatus. Additionally, there are no candidates for evolutionary antecessors to the play-specific warble call in the kea parrot (*Nestor notabilis*; Schwing et al. 2017). As one of the few play-specific calls that have been extensively described in a non-mammal species, the kea's play vocalisation most likely evolved independently. Comparative acoustic analyses across species similar to the methodology of Davila Ross, Owren, and Zimmermann (2009) could shed light on questions of homology versus homoplasy in these signals.

To complicate matters further, not all play vocalisations are the same within a given species, and different vocal signals may have disparate functions within the play context. Many species are described as having several types of play-specific calls. For example, Stevenson and Poole (1982) reported three distinct types of play vocalisations in the common marmoset (*Callithrix jacchus*). Several researchers have described play-specific pants, growls, and barks in domestic dogs (*Canis lupus familiaris*; Bekoff 1995; Simonet et al. 2005; Faragó et al. 2010). Rat researchers have identified different 50 kHz calls that corresponded to specific tactical manoeuvres in play fights (Burke et al. 2018). Future work should investigate which species have multiple types of play vocalisations, and attempt to identify specific functional roles across the types.

Functions of play vocal signals

Most generally, play signals likely evolved to help limit the costs of play. The signals realise this function by reducing costly misinterpretations of impending ambiguous signals and/or behaviours, thus sustaining positive affect, and maintaining or prolonging play bouts. One possible way this is achieved is through metacommunicative signalling – play signals create a context (i.e., indicating ‘this is play’) in which upcoming behaviours are properly interpreted as play rather than aggression (Bateson 1956; Bekoff 1975), though this viewpoint has been criticised as being unnecessarily complicated to explain many nonhuman phenomena (Symons 1978). Play signals can be described as a special class of signals of benign intent. For example, in rhesus macaques (*Macaca mulatta*), a higher-ranking female approaching a lower-ranking female with offspring might signal, through a grunt or a soft vocalisation known as a girney, that she intends no harm to the offspring. She may then approach and have a nonaggressive interaction with that offspring, without the mother acting defensively. These kinds of low-cost signals can be evolutionarily stable if there are repeated interactions between the individuals (Silk, Kaldor, and Boyd 2000). The primary distinction from play signals involves the nature of the behaviour following the signal – interpreting what would otherwise be construed as aggressive intent following the play signal could require sophisticated inhibitory control, if not metarepresentational reasoning.

Most theorists agree that play signals, at a minimum, facilitate play interaction. Research with devocalised rats have lent strong support to this approach. In one study, juvenile rats played more frequently if both partners could vocalise compared to when only one of the partners was devocalised, suggesting that the vocal signals function to encourage or enable play (Kisko et al. 2015b). Other work showed that adult rats were less likely to escalate to aggression (e.g., deliver a bite) during play if both partners could vocalise (Kisko et al. 2015a). Research with adult rats has also demonstrated that certain types of USVs may function specifically to aid in coordination of complex reciprocal ‘moves’ in play, such as attacking and being attacked, while other types of calls appeared to facilitate particularly vigorous or risky behaviours, such as pinning, playful biting, or contact with the neck (Burke et al. 2018). Thus, play vocalisations often function to initiate and prolong playful interactions, and are likely crucial for the coordination of complex play-fighting as seen in rough-and-tumble play. Work with chimpanzees reveals similar functionality, and affords clear comparisons to human laughter. During play, chimpanzees produced laugh-like vocalisations in response to conspecific laughter, and the response laughs may have had unique acoustic features (Davila-Ross et al. 2011). Duration of play was positively associated with the occurrence of these vocalisations, suggesting that they functioned to facilitate play, similar to the way laughter prolongs play and conversation in humans (Schnurr and Chan 2011).

As described earlier, play vocalisations are rather quiet, either as atonal, exaggerated pants or low-amplitude trills or peeps. Their inconspicuous nature is a primary reason they have not been extensively studied acoustically, and are not more thoroughly documented. There are methodological challenges in not only recording the vocalisations effectively, but also identifying signallers during close-contact play. The low-amplitude acoustic form is not surprising if the signals are functioning only within closely interacting dyads or groups. Moreover, there should be selection pressure to avoid risks of predation by not widely broadcasting playful encounters, especially given that interactants are often young, and play distracts from typical anti-predator vigilance (Goedeking 1988). Additionally, if play is

an important bonding activity, advertising it may be costly if third-party conspecifics react aggressively to intervene. These factors likely select for restrained acoustic features such that the play partner can unequivocally detect the signal even during scuffles or noisy chases, but not so noticeable as to attract undue attention from others. In social play such as chasing, there could be additional reasons we might expect quiet signalling. For example, stealth predators like cats might be expected to use quiet signalling as they calibrate pursuit behaviour. In fact, several species of cats have been observed using inconspicuous, hiss-like, atonal vocalisations as play signals (Fagen 1981). Overall, quiet signalling during play makes it fairly clear that the signals are transmitted only between the interacting partners, suggesting a play facilitation function, without a broadcast function. That is, only the interactants are able to hear the signalling, and it benefits them by lengthening play time (Burke et al. 2020).

While play vocalisations tend to be quiet, ‘conspiratorial whispers’ (Krebs and Dawkins 1984), there are exceptions. Even with selection for inconspicuousness, formal models suggest that signal detection costs must be considered for senders, receivers, and eavesdroppers, and that some circumstances can result in greater magnitude signals without selection for broadcasting (Johnstone 1998). For example, play was more likely to escalate into aggression in adult rats when one play partner was devocalised, showing the high stakes of failing to perceive play vocalisations (Kisko et al. 2015b; Burke et al. 2017a). Interestingly, 50 kHz USVs of rats during play may be uniquely suited to balance the competing costs of detection from predators and non-detection from conspecifics, as they dissipate rapidly (Brudzynski 2019).

In other circumstances, there could be selection for wide broadcast. While clearly in the minority, some species generate conspicuous play signals, including the play peeps of squirrel monkeys (*Saimiri sciureus*), the barks of domestic dogs (*Canis lupus familiaris*), seals (*Phoca vitulina*), and sea lions (*Zalophus californianus*), the play-trumpets of African elephants (*Loxodonta africana*), the warble of kea parrots (*Nestor notabilis*), and the loud laughter of humans (Peterson and Bartholomew 1969; Biben et al. 1989; Feddersen-Petersen 2000; Poole 2011; Bryant 2020a). There is no single account that likely explains loud play vocalisations across all of these species, but any explanation must address both the apparent low costs of broadcasting to potentially dangerous eavesdroppers and the possible benefits of signalling to third-party conspecifics. Notably, many species with loud play vocalisations are large-bodied, and are not particularly vulnerable to predation. While somewhat unique acoustically in the category of animal play vocalisations, we can obtain great insight into the nature of human laughter by identifying commonalities across species in acoustic form and communicative function. Moreover, form-function comparisons can help identify possible homoplasies, as particular acoustic features might serve similar specific play-related functions across disparate species due to evolutionary convergence. We will return to the issue of loudness in our discussion of human laughter.

Laughter as a human play vocalisation

The anthropoid apes, as we have seen, likewise utter a reiterated sound, corresponding with our laughter, when they are tickled, especially under the armpits.

- Charles Darwin (1872), p. 199

It has long been recognised that human laughter bears a strong resemblance to play vocalisations in the great apes (Darwin 1872), but only fairly recently has the deeper connection been made to play vocalisations across mammals other than primates (Panksepp and Burgdorf 2000; Provine 2000; Gervais and Wilson 2005). However, even compared to its counterparts in our closest living relatives, laughter in people has evolved into a much more complex signal (Scott et al. 2014). People laugh in almost any possible situation, and in contexts associated with any identifiable emotional state. For instance, we have the potential to laugh when we are in despair, disgusted, joyous, or bewildered. Many philosophical works have focused on laughter's so-called dark side, with connections to teasing, taunting, and *schadenfreude* (for a review see Provine 2000). Despite this extreme flexibility, most instances of laughter can be reasonably classified as playful at some level. For example, if we consider the criteria of play described earlier (Burghardt 2005), cases of verbal taunting or teasing, while often construed as negative, certainly qualify. Teasing is non-functional in the short term, rewarding for the teasers (and potentially the target), modified from actual verbal aggression, repeated over time, and generally occurs during unstressed and ordinary moments. Laughter can help initiate and prolong a teasing attack, make it feel non-serious and playful, and can even elicit laughter in targets despite their lack of desired participation (Glenn 2003; Schnurr and Chan 2011; also see Eckert et al. 2020 for a comparative perspective on playful teasing).

The most obvious manifestations of playful human laughter occur in contexts associated with humour, such as tickling and joking. The case of tickling is, of course, the closest context that connects laughter to other primate play vocalisations – exaggerated panting mixed with squeaks and grunts, directly triggered by rough-and-tumble play – but its complexity is apparent even in this situation. During tickling, human laughter can be intermixed with other vocalisations that communicate distress, including screaming and crying – even unadulterated laughter does not necessarily index pleasure. In the case of ordinary conversational joking (as opposed to scripted jokes or formal comedy), laughter can act as a means for speakers to inform receivers of the presence of a joke, or for receivers to signal the recognition of one. The completion of a natural (i.e., conversational) joke turn can be effectively conceptualised as a form of encryption-decryption. That is, the actual referent in an utterance, or set of utterances, is unstated, and spontaneous *colaughter* can act as a signal of mutual knowledge (Flamson and Barrett 2008; Flamson and Bryant 2013). The case of conversational joking might represent the point of departure for human laughter as a separate kind of vocal signal from its nonhuman play vocalisation precursor.

As an emotional expression, spontaneous laughter is generated by a vocal production system shared across all mammals, as opposed to volitional laughter that is produced by a speech system unique to humans (Jürgens 2002; Ackermann et al. 2014). The conserved nature of vocal emotions provides the best *prima facie* evidence that ape laughter evolved from a play vocalisation in a mammalian common ancestor that lived at least 100 MYA. But humans are unique across the great apes in our capacity for speech, generated by a volitional vocal production system that other apes only reveal with debated limitations (e.g., Pisanski et al. 2016; Lameira 2017). We can control our vocal apparatus to produce an amazing range of sounds, and do so in ways that mimic, sometimes with dramatic accuracy, sounds around us. One of the targets of selection in the development of this ability was likely the imitation of genuine emotional vocalisations: deliberate crying,

screaming, and laughing that is decoupled from the emotional triggers required for spontaneous production (Bryant and Aktipis 2014; Bryant et al. 2018).

Volitional control over our vocal production co-evolved with language and many aspects of human culture and cooperation, though comparative data suggest some aspects trace back to before the appearance of modern humans (Pisanski et al. 2016). Laughter has certainly played an important role in our sophisticated communicative capacity. Within that complex milieu, the ancestral function of play still looms large – volitional laughter retains some important characteristics of play vocalisations we see in other mammals. In humans, natural conversation can be an important context of play. Like teasing described earlier, many conversational structures satisfy Burghardt's (2005) criteria, and constitute playful interaction that requires particular play signalling. Laughter plays an important role in the timing and unfolding of conversational behaviour, including the signalling of turns during talk, backchanneling, signalling emotional investment in the interaction, and regulating conversational flow (Jefferson 1979; Vettin and Todt 2004).

Functionally, a controlled (i.e., volitional) form of laughter fulfils many pragmatic needs in conversation (Pisanski et al. 2016; Bryant 2020a). In contrast, spontaneous laughter can interrupt the speech production system and is thus not well-suited to operate during discourse (McGettigan and Scott 2014). Volitional laughter is deployed strategically, in rule-governed ways around linguistic units (Provine 1993), and in a manner quite similar to how play vocalisations operate in nonhuman animals, such as managing turn-taking, inducing positive affect, and regulating the flow of play. For example, when using indirect language (e.g., verbal irony, parody, and other figurative devices) that relies heavily on inferential communication, laughter can help listeners understand speakers' actual communicative intentions (Bryant 2011; Bryant 2020a). These instances are often experienced as humorous and are easily construed as verbal play, including role-playing and reciprocity. Laughter can mark an utterance as indirect, typically resulting in a relevant response that engages the speaker in a pretence-based, play-like bout (Gibbs 2000), also often marked by responsive laughter (Bryant 2011; Schnurr and Chan 2011). Contrary to folk intuitions, speakers produce laughter much more frequently than receivers (Provine 2000; Vettin and Todt 2004). Speakers mark their own ambiguous speech with benign or playful intent, mirroring the way that nonhumans produce play signals before an ambiguous play attack. More generally, laughter functions to limit the cost of indirect speech (Sally 2003; Pinker et al. 2008), which is quite similar to the way that nonhumans use play signals to reduce the potential cost of an interaction escalating to aggression.

One consequence of ongoing verbal play between two or more people is the recurring colughter that is readily audible to third parties. Most laughter occurs in group contexts, and this fact might help explain one of the unusual acoustic features of human spontaneous laughter: it is typically quite loud. As described in the introduction, children's play is accompanied by a familiar cacophony of laughter and screaming. Adults also frequently engage in loud colughter, whether at parties, in bars and restaurants, or just during ordinary conversation. Human laughter has all the acoustic hallmarks of a signal designed for wide broadcast: alerting components (i.e., high amplitude and high frequency onset), conspicuousness, and repeated elements with small repertoires (Wiley 1983). Additionally, it is contagious – hearing laughter is the

best trigger for spontaneous laughter (Provine 1992). Overall, the acoustic form of colaulter suggests a group chorusing function (Bryant et al. 2020). While few (if any) nonhuman play signals appear to have this chorusing function, some play signals are known to be contagious among dyads, as in the case of rapid facial mimicry of primate play faces or the contagion of play vocalisations in keas (Mancini et al. 2013; Schwing et al. 2017; Palagi et al. 2019).

What does it mean when people are laughing together in a group? As in our previous example of encryption and humour, when two or more people share an inside joke they are often triggered to laugh together. In doing so, the group is implicitly revealing that they have shared information, which may be due to strongly bonded relationships or, at a minimum, shared cultural references. The positive emotions and proximate physiological rewards associated with successful humorous interaction and colaultering bouts (e.g., Manninen et al. 2017) drive what might be an honest signal of affiliation that is often broadcast fairly widely to others nearby. Research shows that people are sensitive to it. When presented with very brief (~ 1 s.) audio presentations of colaulter, listeners from around the world could distinguish between established friends and newly acquainted strangers (Bryant et al. 2016). Even infants as young as five months associated friendly colaulter with affiliative behaviour in others (Vouloumanos and Bryant 2019). Colaulter also signalled affiliation more reliably than another kind of co-occurring vocalisation – overlapping talk – even when the talk samples were over twice as long in duration (Bryant et al. 2020). Colaulter might comprise a derived signal of affiliation that allows groups of friends to communicate to other individuals. In our evolutionary past, there could have been positive selection for signalling group affiliation among large, interconnected social networks. Colaulter fulfils this function efficiently, possibly representing a unique turn in the evolution of primate play signals associated with the emergence of language and complex, cooperative sociality among humans.

Conclusion

The regulation of social play in many species often requires the use of visual and vocal signalling. These signals help animals clearly communicate intentions during interactions where misunderstandings could have costly consequences. In a play fight, for example, the ongoing negotiation of participants' roles facilitates continued interaction, ultimately helping to calibrate physical development and prepare animals for future aggressive encounters. Close examination of play vocalisations across disparate species helps illuminate the nature of human laughter, one of our most common and mysterious vocal behaviours. Laughter helps people negotiate relationships, manage emotional experiences, and engage in complex social interactions both linguistically and nonverbally. The social uses of human laughter are innumerable, including ancestral functions associated with play, affiliation, and positive affect, as well as derived functions that occur during conversation. Volitional laughter can be used deceptively to induce affect in ways that manipulate receivers against their interest (Bryant and Aktipis 2014; Bryant et al. 2018), but can also be used as a pragmatic device to help facilitate positive emotional connections between people. Additionally, people laugh in large groups, possibly as a means of intergroup signalling. Overall, human laughter

contains contextual and acoustic features that make it somewhat unique across mammals, and even great apes.

Our comprehensive literature review reveals that vocal signals during social play are quite common across mammal species, and some birds, further challenging the once 'conventional wisdom' that animal play is silent (Fagen 1981, p. 149). Still, much more comparative research is needed to understand the phylogeny of play vocalisations. Different factors leading to the evolution of play signals might be associated with distinct evolutionary trajectories. For example, the capacity for social play and its appearance across animals might be the product of deep neurological and behavioural homologies that underpin social interaction more generally. But constraints on vocal signalling evolution could result in variable appearances of play-specific vocal signals across distant taxa. Even if play is homologous between any two given species, their play vocalisations might be convergent due to different vocal evolutionary histories, or changing ecologies that afford selection for particular kinds of vocalisations (or their absence altogether). More research examining the social and ecological contexts of species with play vocalisations will help shed light on the evolutionary factors that preclude selection for both the presence of play vocalisations and their particular acoustic features.

There are many methodological problems that must be overcome to properly study play vocalisations. As noted earlier, a high proportion of known play vocalisations are very quiet, so it is a certainty that many species generate these signals but the behaviour has not been documented in the scientific literature. Fortunately, technology is improving and wireless audio recording possibilities are increasing (e.g., Gayk and Mennill 2020). Additionally, sensing technologies developed for animal welfare (for reviews see Jukan et al. 2017; Neethirajan 2017) could be potentially adapted as a means of gathering continuous emotional and behavioural data for a more comprehensive approach to a variety of communication phenomena, including play signals. A large proportion of the studies we collected have descriptions of play vocalisations only as an aside, but greater focus on specific acoustic properties and behavioural patterning of play vocalisations will help answer outstanding questions about the evolution and function of these signals.

Further research is also needed on the sources of variation between species in the presence and frequency of play vocalisations. With more rigorous comparative criteria for identifying play, we should be able to include additional species, including taxa described here that have been commonly overlooked in discussions of laughter and play signalling. For instance, cetaceans, pinnipeds, and other marine mammals that rely heavily on acoustic communication are good candidates for the use of vocal play signals, but research to date is sparse. This is, in part, likely due to a common resistance to describe behaviours as 'playful' in these animals (Hill et al. 2017).

The study of play vocalisations is part of a much larger enterprise of understanding the nature of animal communication systems, and the related puzzle of human communication. Laughter might be one of the best examples of communicative behaviour that affords comparative analysis, while remaining deeply embedded within our uniquely human language and culture. Recent developments in comparative neuroanatomy have provided fascinating insights into the origins of volitional voice modulation, and future research will undoubtedly lead to new discoveries regarding the many connections between human and nonhuman vocalisations. There is still much to learn, so keep laughing.

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