Reviews

Animal play and animal welfare

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Play has long been identified as a potential welfare indicator because it often disappears when animals are under fitness challenge and because it is thought to be accompanied by a pleasurable emotional experience. But animal play is a vexing behavioural phenomenon, characteristically flexible and variable within and between species, with its proximate mechanisms and ultimate functions still not fully understood. Its relationship to animal welfare is therefore complex and merits a focused theoretical investigation. We review evidence on four aspects of the play–welfare relationship: first, that play indicates the absence of fitness threats; second, that play acts as a reward and flags up the presence of opioid-mediated pleasurable emotional experiences; third, that play brings immediate psychological benefits and long-term fitness and health benefits, and thus improves current and future welfare; and finally, that play is socially contagious and therefore capable of spreading good welfare in groups. On this basis, we argue that play does indeed hold promise as a welfare indicator and also as a tool to improve it; but we also point to difficulties in its study and interpretation, and identify some unresolved questions. As a welfare indicator, play may signal both the absence of bad welfare and the presence of good welfare, thus covering a wide range of the welfare spectrum. However, play can also increase in stressful situations, in response to reduced parental care, or as a rebound after a period of deprivation and therefore does not consistently reflect favourable environmental conditions. A better fundamental understanding is needed of the varied ultimate functions and proximate mechanisms of play, and the species-specific play patterns of captive animals, in order to be able to explain exactly what an animal's play behaviour tells us about its welfare state, and whether and how play might be applied as a tool to improve welfare.
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To suggest a relationship between the play behaviour of animals and their welfare is hardly novel. Play has long been identified as a potential indicator of the current welfare state of an animal (e.g. Fagen 1981; Lawrence 1987). It is easy to recognize, present in a wide array of mammals and can be measured noninvasively (Fraser & Duncan 1998; Špinka et al. 2001; Barnard 2004; for other taxa see Fagen 1981; Burghardt 2005); it is often expressed in the absence of fitness threats and can drop out of the behavioural repertoire when conditions become more challenging (Lawrence 1987; Fraser & Duncan 1998; Špinka et al. 2001; Dawkins 2006); it is also commonly linked to the experience of positive emotions in animals (Fraser & Duncan 1998; Špinka et al. 2001; Barnard 2004; Burgdorf & Panksepp 2006) as it has long been in humans (e.g. Clark & Miller 1998). In human children, for example, play inhibition is one of the core symptoms of depression, both in

standardized play tests and in free play situations (Lous et al. 2002). The most recent review of positive emotions in the context of animal welfare assessment therefore singled out play behaviour as one of the three most promising indicators of positive emotions in captive (to include 'domestic') animals (Boissy et al. 2007). Play behaviour thus appears to have the potential to flag up challenging conditions, in which an animal's welfare may be compromised, as well as favourable situations, which induce positive emotions and good welfare. Furthermore, playing can have immediate, delayed and/or long-term benefits and thus cause welfare improvements, not just reflect them. Yet a systematic theoretical or experimental investigation of the relationship between animal play and animal welfare is lacking. The main purpose of this review therefore is to provide a theoretical analysis of how an animal's play behaviour relates to its welfare. Within this, we put the case that play can not only result from good welfare but also cause it.

Defining 'play' is difficult because it covers many behavioural categories, varies considerably between and within species, and its single or multiple functional significance is still being debated (e.g. Bekoff & Byers 1998; Power 2000; Špinka et al. 2001; Burghardt 2005). In the absence of a widely agreed functional or structural

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definition of play, authors have sought to capture its essence using lists of shared characteristics or criteria. Burghardt's (2005) five essential criteria work well for our purposes here. For him, play (1) is a behaviour that is not 'fully functional' (by this is meant it includes elements 'that do not contribute to current survival'); (2) is 'autotelic', that is self-rewarding (see also the section below on Animal play and experiencing 'pleasure'); (3) differs in structure and/or timing from the adult, 'serious' form of the behaviour; (4) is performed 'repeatedly', but not stereotypically; and (5) is initiated when the animal is in a 'relaxed field' (by this is meant there are no immediate threats to the animal's fitness). The main types of play are social play directed at a conspecific (as in Burghardt 2005), locomotor-rotational (alone or in company, see Wilson & Kleiman 1974) and object play (see Fagen 1981); examples are given in Table 1.

Defining animal welfare is no easier. Animal welfare science has to bridge the gap between the ethical values that drive our concerns about how well captive animals fare and the scientific investigation of animal physiology, behaviour, health/disease and psychology (including emotions, motivation, sentience/consciousness; Fraser et al. 1997). Animal welfare scientists and activists therefore take a variety of views on what determines an animal's welfare. The three most commonly included determinants are: (1) the animal's subjective emotional experiences; (2) its physical health and biological functioning; and (3) the extent to which the animal is able to live in ways that are natural for its species (Fraser 2009; Yeates 2010). In this review, we side with the subjective experiences and health view (Dawkins 2008), that is we consider animal welfare to be improved when positive emotions and healthy biological functioning increase, or negative emotions, health problems and other biological malfunction decrease.

In the following, we first explore the tenet that animal play indicates the absence of fitness threats; we then examine whether play indicates the presence of 'pleasure', discuss suggested benefits of play for immediate and future biological functioning, consider the contagious nature of play behaviour and its implications for animal welfare, and discuss the variability of play as a problem for its use in animal welfare assessment and improvement. Finally, we indulge in some speculation and summarize how the unusual nature of play as compared to other behavioural categories affords it its unique position in relation to animal welfare.

ANIMAL PLAY AS INDICATING ABSENCE OF FITNESS THREATS?

Play behaviour is characteristically labile: changes in the frequency of play are closely linked to changes in prevailing environmental conditions, and play is also easily interrupted by immediate threats to an animal's fitness (Fagen 1981; Martin & Caro 1985; Burghardt 2005). One example is the sensitivity of play behaviour to changes in food availability as demonstrated in field and experimental studies of primates, ungulates, rodents and carnivores. Loy (1970), for example, observed a 17-fold drop in play behaviour in a free-living colony of rhesus monkeys, Macaca mulatta, on Cayo Santiago Island as a result of an acute food shortage lasting 22 days. When Müller-Schwarze et al. (1982) reduced the milk supply of bottle-fed white-tailed deer fawns, Odocoileus virginianus, by 33%, they found a concomitant 35% reduction in play behaviour, while Siviy & Panksepp (1985) recorded a three-fold decrease in play pinning after a 24 h food deprivation in juvenile rats, Rattus norvegicus. In dairy calves, Bos taurus, weaning and a reduced milk allowance preweaning reduced playful running (Krachun et al. 2010). On the other hand, experimental food supplementation more than doubled the rate of play of free-ranging meerkats, Suricata suricatta, compared to nonprovisioned controls (Sharpe et al. 2002). Other environmental factors shown to be associated with reduced play include poor weather conditions (Rasa 1984), overcrowding (e.g. in cats, Felis catus; Leyhausen 1979; but see Tacconi & Palagi 2009), and injury hazards such as cactus spines (Berger 1979). Play behaviour may also decrease and can disappear completely in injured, unhealthy animals, and re-emerge as they recover (Fagen 1981). For instance, play is depressed for at least 3 days after castration in 1-week-old domestic lambs, Ovis aries (Thornton & Waterman-Pearson 2002). Furthermore, play may be quickly dropped in favour of a behaviour that the animal is currently strongly motivated to perform because of its associated fitness consequences. In Cordoni's (2009) study, captive adult wolves, Canis lupus, exhibited less solitary and social play during mating than in nonmating periods, and during feeding than in postfeeding periods. Renouf (1993) similarly found solitary locomotor play reduced in harbour seals, Phoca vitulina, during the mating season. Perceived, rather than actual, fitness threats can also affect play. Cat odour, bright light and lack of shelter, for instance, reduce play in rats (Panksepp et al. 1984; Vanderschuren et al. 1995a; Panksepp & Burgdorf 2010).

Findings such as these are widespread, which has led many to suggest that play indicates that the subject animal is in a 'relaxed' state in the sense of being free from sickness, hunger, injury, predation risk, thermal stress or other challenges to its fitness including lost mating opportunities (e.g. Martin & Caro 1985; Burghardt 2005; and earlier references therein). This relationship has since been more explicitly linked to animal welfare by Lawrence (1987) and Fraser & Duncan (1998; see also Boissy et al. 2007). Lawrence (1987) argued that because of its lability, play could be viewed as a 'luxury' behaviour. This would be a behaviour performed only in situations when the animal's 'proximate needs' are met, and thus its welfare is not compromised (Dawkins 1983, 1990). Fraser & Duncan (1998) presented a related argument for play as a welfare indicator. They distinguished between 'need situations' (for example, escape behaviour in response to predation threat), that is situations in which a particular behaviour is performed because it is of great benefit (rather than of low cost), and 'opportunity situations', where actions are performed because their

Table 1
Examples from captive (domestic) animals to illustrate the three main types of play

Play type	Species	Examples	Description	Source
Locomotor-rotational	Domestic pig, Sus scrofa	Pivot	Jump on spot to face in a different direction (rotation of at least 90°)	Newberry et al. 1988 Donaldson et al. 2002
		Hop	Jump up and down on the spot while facing in one direction	Newberry et al. 1988
		Scamper	Sequence of two or more forward hops in rapid succession	Newberry et al. 1988; Donaldson et al. 2002
Object play	Domestic cat, Felis catus	Object play	Paw, pat or bite an inanimate object	Bateson & Young 1981
Social play	Laboratory rat, Rattus norvegicus	Pounce	Subject rat approaches another and attempts to nose or rub the other's nape of the neck	Vanderschuren et al. 1997
		Play pinning	One rat lies with its back on the floor with subject rat standing over it	Vanderschuren et al. 1997; Panksepp 1998

costs have become low (rather than their benefits high). Fraser & Duncan (1998) identified play as one such behaviour whose performance cost may be low when an animal's other needs are satisfied, and thus its welfare is not compromised.

As these examples illustrate, the evidence for play decreasing or disappearing from the repertoire when environmental conditions are challenging an animal's fitness status is strong. Boissy et al. (2007) reviewed research showing that the 'lability of play' argument given above also applies to domesticated, captive animals. It is therefore tempting to assume that play is always a 'luxury' behaviour with its levels indicative of an animal's welfare status. Animal welfare is often represented in a simplified version as a continuous state on a scale ranging from very poor to very good (e.g. Broom 1991). In this view, play behaviour would drop out of the behavioural repertoire at the transition between good to poor welfare; and its presence would indicate the absence of poor welfare.

However, there are some dissident cases. Bateson and colleagues (Bateson et al. 1981, 1990; Bateson & Young 1981) showed that the restriction of milk provisioning and maternal care in kittens through separation from their mother increases play compared to controls. Maternal undernourishment and interrupting lactation with bromocriptine had the same effects. Moreover, the more a particular mother cat reduced her care, the higher was the play increase in her litter. Bateson et al. (1981, 1990) argued that this is an adaptive response since the restriction of investment by the mother signals an unfavourable environment in which the kittens (in the wild) would be forced to full independence at an earlier age. The early weaned kittens therefore should play more while they are still provided with solid food and protected by the mother and have the company of their siblings. A similar case has been made for increased play rates in rat pups of undernourished or simultaneously pregnant dams (Smith 1991) and in rhesus monkey yearlings exposed to a sudden decline in maternal care caused by the birth of a younger sibling (Devinney et al. 2003). Animals may also use play interactions to reduce social tension and play levels can thus increase during socially stressful periods such as immediately before feeding in captive bonobos, Pan paniscus (Palagi et al. 2006) or when an unfamiliar male is being integrated into a group of resident sifaka, Propithecus verreauxi (Antonacci et al. 2010).

Increased play frequencies may also result from challenging conditions if there is a rebound effect in response to a new opportunity for play. Wood-Gush et al. (1990) showed that domestic pig, Sus scrofa, litters from barren pens played more than piglets from enriched pens when they were given access to a novel pen adjacent to their home pen. Calves, similarly, will gallop and buck (forms of locomotor-rotational play) more after a period of confinement than unconfined controls (Jensen 1999). Some methods of testing 'playfulness' in juvenile laboratory rats may trigger a rebound response because amounts of social play are recorded during short opportunities for social companionship after periods of complete isolation lasting a day or more (Ikemoto & Panksepp 1992; Loranca et al. 1999). Social isolation is used to 'heighten playful activity' (Loranca et al. 1999) but it may also create a confounding rebound effect on social interaction unspecific to play. That said, preventing a young rat from playing with a companion by allowing social contact but separating the two with a wire mesh still produces a play increase after separation, suggesting the rebound is specific to play (Holloway & Suter 2004). Finally, studies on the ontogeny of rat play have shown increases in social play above baseline levels after lesioning of parts of the olfactory system (Beatty et al. 1982; Loranca & Salas 2001). Increased play in such cases of sensory dysfunction and brain trauma may be explained by a disruption of the neurological mechanisms modulating social play, and are unlikely to signal a welfare improvement.

It would seem appropriate then to qualify the statement that play is exclusively a 'luxury' behaviour, labile under fitness challenge, and to question the assumption that the presence of play or its increase invariably indicates good or improved welfare. Taken together, the studies reviewed here suggest that under fitness challenge, play may (1) give way to behaviours that are more urgent because of their immediate fitness consequences, (2) increase because it buffers an animal against the adverse effects of worsened conditions now or in the future, or (3) be suppressed initially but increase above baseline under rebound later.

Furthermore, a fitness challenge from deterioration of environmental conditions can also affect play quality rather than merely its quantity. This effect is less well documented but one example comes from Barrett et al.'s (1992) analysis of the effects of rainfall on play in an Ethiopian population of gelada baboons, Theropithecus gelada. Overall levels of play behaviour predictably positively tracked rain levels. A decline in rainfall, however, also meant a shift from high-energy play elements such as play boxing and wrestling towards play actions involving less physical movement (e.g. object play and play biting). The quality of an animal's or a group's play behaviour may thus also provide information about their welfare. Future research might thus profitably investigate the relationship between play 'content' and welfare (see also Pellis & Pellis 2010) as well as attempt to identify those play types and their contexts for which increased frequency invariably means improved welfare.

ANIMAL PLAY AND EXPERIENCING 'PLEASURE'

Understanding whether and how animals experience emotions is seen by many as the key to improving animal welfare. Recent advances in the study of animal emotion and affective neurosciences (e.g. Berridge 2003; Dalgleish 2004; Paul et al. 2005; Rolls 2005; Mendl et al. 2010) have therefore not gone unnoticed by animal welfare science (Boissy et al. 2007; Yeates & Main 2008; Mendl et al. 2009; Kalbe & Puppe 2010). In this section we introduce selected behavioural and neurobiological evidence that suggests play works as a reward and may be accompanied by the pleasure-like emotional state that accompanies reward consumption.

Play is typically spontaneous in as much as its performance often appears independent of external stimulation; it is self-rewarding or 'autotelic' (Burghardt 2005). By this is meant that it is displayed for its own sake rather than to achieve a consummatory goal; the reward to the animal is in the expression of the behaviour itself. Classic evidence for the autotelic nature of play comes from an early series of experiments with young chimpanzees, Pan troglodytes, (Mason et al. 1963, cited in Vanderschuren 2010) and subsequent conditioning studies in rats, in which social play worked as the reinforcing reward. Mason et al. (1963) tested the preferences of chimpanzees for social play or other types of social interaction over different types of food. Subjects were trained to press different levers for access to food and to a social interaction (either play or petting), and levels of hunger and types of food were varied. The results showed play to be a stronger reinforcer than petting or a nonfavoured food such as chow, and as strong a reinforcer as the most highly valued food (fresh fruit). Humphreys & Einon (1981) trained rats in spatial discrimination T-maze tasks using the opportunity to meet a companion as a reinforcing reward. Companions were either playful, amicably sociable but not playing (following amphetamine or chlorpromazine injection), or unsociable and not playing. Rats learnt the discriminations between different companions as quickly as a food/no food discrimination. They preferred a playful companion over a nonplaying but sociable companion, and a nonplaying one over an unsociable one,

suggesting that play increased the reinforcing power of the companions (Humphreys & Einon 1981). In a conditioned place preference test, Calcagnetti & Schechter (1992) similarly tested whether a previous place (chamber) preference could be overturned by providing subjects with a social play partner in their previously nonpreferred chamber. The previously preferred chamber now contained a social partner rendered unable to play by scopolamine injection. After conditioning, subjects dramatically increased the time they spent in the previously nonpreferred chamber.

Social play, then, acts as a 'reward' in the sense that it is something 'an animal will work for' (Rolls 2005) or 'wants' (Berridge & Robinson 2003; Dawkins 2008). In the view of Berridge and colleagues, this 'wanting' or motivational psychological component of reward is distinct from its hedonic properties, that is, from the positive emotions that cause a reward to be experienced as pleasurable (e.g. Berridge & Robinson 2003; Berridge & Kringelbach 2008; for a different view see Rolls 2005). Of relevance to our purposes here is that the subcortical brain areas and opioid neurotransmitter systems that mediate the hedonic properties of rewards overlap with those involved in social play in rats (Panksepp 1998; Vanderschuren 2010). The injection of an opioid agonist such as morphine into the shell of the nucleus accumbens, for example, increases behavioural hedonistic responses in rats after tasting a sucrose solution (tongue protrusion and paw licking; Peciña & Berridge 2000). Opioid agonists also increase social play in rats. Normansell & Panksepp (1990), for example, tested the effects of peripherally administered morphine and the opioid antagonist naloxone on the expression of social play in the goal box of a T-maze task where play was used as a reinforcer. Morphine increased and naloxone decreased social play. Social play can also, conversely, increase opioidergic activity in the nucleus accumbens suggesting that it may not only reflect changes in opioid levels but also cause them (Vanderschuren et al. 1995b). Since then, many studies have confirmed the central role of brain opioids in the regulation of social play in rats. In summary, opioid agonists increase social play and antagonists decrease it. Interested readers are referred for further details (also on the involvement of the dopaminergic system) to reviews by Vanderschuren et al. (1997), Panksepp (1998), Siviy (1998) and Vanderschuren (2010).

But again, we wish to sound a note of caution. Evidence for opioid involvement in animal play is largely confined to social play in rats with one study on common marmosets, *Callithrix jacchus* (e.g. Panksepp 1998; Guard et al. 2002; Vanderschuren et al. 1997; Pellis & Pellis 2009; Vanderschuren 2010). It suggests a proximate mechanism for endogenously reinforcing a behaviour for which some fitness-enhancing benefits and associated rewards may be delayed (e.g. increased sexual behavioural competence in adult male rats resulting from play fighting as juveniles, Pellis & Pellis 2009; see section below on Functions of play and associated welfare benefits). Some delayed and long-term fitness benefits have also been hypothesized to be ultimate functions for object and locomotor-rotational play (see section below on Functions of play and associated welfare benefits). An immediately rewarding, pleasurable positive emotion mediated by brain opioids may thus also accompany these types of play. But whether they are indeed similarly influenced and accompanied by opioid activity is currently not fully understood.

Note also that social play fighting can play a role in asserting dominance (e.g. in pigs: Newberry et al. 1988; in rats: Smith et al. 1999; in dogs, *Canis familiaris*: Bauer & Smuts 2007). As such it may be accompanied by negative affect caused by (social) stress (Enkel et al. 2010; Mendl et al. 2010), not just by positive affect. Finally, the distinction between play fighting and real fighting may be blurred (Newberry et al. 1988; Fry 1990; Watson 1998; Šilerová

et al. 2010). Social play that resembles, and can escalate into, real conflict behaviour incurs a fitness risk, and play signals therefore often increase in social situations where the risk of misunderstanding is high (Bekoff & Allen 1998; Palagi 2009; Tacconi & Palagi 2009). Play fighting and other forms of social play may thus not always indicate that animals are experiencing pleasure and good welfare. Further research is clearly needed into the role of opioids in the social play of species other than the rat, and into their role in locomotor-rotational and object play.

FUNCTIONS OF PLAY AND ASSOCIATED WELFARE BENEFITS

Play is not for free. Despite being performed mostly under favourable conditions (see above), it costs the animals time and energy (Sharpe et al. 2002) and exposes them to injury, predation (Harcourt 1991) and disease transmission (Kuehl et al. 2008). Its actual fitness costs in wild animals have been suggested to vary from negligible (Martin 1984; Caro 1995) to substantial (Harcourt 1991) in different species and situations. We do not discuss the fitness costs of playing in this review, because they are of less importance to the welfare of captive animals with which we are primarily concerned. Predators, food shortages and other environmental fitness challenges are usually absent in captive environments, and captive animals thus commonly have both energy and time in abundance.

If play carries any costs, it follows that it must also bring fitness benefits. If not, playful individuals would be at an evolutionary disadvantage to conspecifics that were not playing at all. Many different hypotheses have been proposed for the adaptive value of play (Bekoff & Byers 1998; Špinka et al. 2001; Burghardt 2005), and a thorough review of them is not the purpose of this paper. Instead, we summarize here the main putative functions of play, then discuss their welfare implications.

Hypotheses on the functions of play can be loosely divided into two categories: those centred on its long-term benefits and those focusing on immediate fitness benefits. The first category covers any enhanced skills, competencies and somatic qualities of the animal resulting from playing. Such effects may persist for a limited or long time, or even for life. Most theories in the ethological and psychological traditions fall into this category as they assumed that play mainly brings long-term benefits: training behaviours in their 'play-form' at little fitness risk during infancy or in the juvenile period increases their efficiency and competence in the equivalent adult 'serious' form. This assumption was based on the observation that play occurs mainly when animals are young, does not seem to have any immediate goals, and contains behavioural patterns similar to adult ones (Groos 1898; Fagen 1981; Smith 1982).

Three major types of hypothesis fall into this category. The first are hypotheses proposing that playing supports or channels somatic development. Byers & Walker (1995), for example, suggested that play serves to guide synaptogenesis in the cerebellum and to fine-tune the differentiation between slow and fast skeletal muscle fibres. Second, play is thought to train species-typical behaviours used later in life. Pellis & Pellis' (2009) analysis of play fighting in male rats, for instance, suggests that play fighting improves the efficiency of male sexual behaviour through fine-tuning the compensatory movements in relation to the movements of the female. Finally, play behaviour is also thought to enhance more generic physical and emotional skills that can be used across many situations. Špinka et al. (2001) and Pellis & Pellis (2009), for example, proposed that higher emotional resilience and kinematic flexibility throughout life is acquired through the experience of unpredictability in play. However, it is becoming increasingly clear that adult animals also play (e.g. Watson 1998), that many play elements do not resemble any adult patterns (e.g. Renouf 1993;

Petrů et al. 2009) and, most crucially, that play behaviour often precedes, accompanies or follows behavioural patterns that matter in the present (such as feeding, aggression or sexual behaviour, e.g. de Oliveira et al. 2003; Palagi et al. 2006). Researchers now therefore consider play as having immediate benefits as equally as plausible as it having delayed benefits (Martin & Caro 1985; Burghardt 2005).

Our second category of the fitness consequences of play thus comprises more recent hypotheses that propose immediate benefits. Benefits are 'immediate' in that they are linked to the animal's current situation: the playing animal obtains or achieves something that is relevant here and now but may fade away if the situation changes. Here too, hypotheses can be sorted into three broad classes: (1) some authors suggest play helps the animal to obtain useful information about the environment (e.g. Stamps 1995), about group members (Feuerriegel 1997; Cordoni 2009) or about itself (through self-assessment, Thompson 1998), or it may enable the animal to provide information about its development or status, to its parent(s) for instance (Fagen 1992); (2) play may be a way of self-medication, for example, to self-administer endogenous opioids (Pellis & Pellis 2009); and (3) the animal may influence its current social situation through play, for example, to reinforce its dominance status (Feuerriegel 1997; Bauer & Smuts 2007), to reduce tension around feeding (e.g. Palagi et al. 2006) or to turn a stranger into a familiar animal (Antonacci et al. 2010).

Empirical evidence remains patchy for most hypotheses summarized above, and general consensus on the adaptive value of play clearly still eludes us. This has several reasons. The first is that mammalian play behaviour has diversified widely to serve different specific functions in different species (Burghardt 2005; Pellis & Pellis 2009). Reaching consensus about the one global function of play thus seems a tall order. Second, putting together strong evidence on any given putative function of play is methodologically difficult. Experimental approaches that have the potential to provide direct evidence for any causal effects of play are hampered by the practical challenge of manipulating play without affecting other behaviour patterns (e.g. Donaldson et al. 2002; Pellis & Pellis 2009). Finally, the positive relationship between the quantity of play and the resulting benefits may not be linear and continuous. For instance, it is possible that in some species a minimum threshold level of play is all that is necessary for a developmental effect such as muscle cell differentiation (Byers & Walker 1995). Where this is the case, a study may fail to reveal any beneficial effect if the observed variation in the quantity of play falls entirely below (or above) the threshold.

Given this state of knowledge on the functional benefits of play, what can be said about their implications for the welfare of captive animals? We first consider the delayed, long-term play benefits. Almost by definition, if engaging in play strengthens some future somatic properties, enhances skills or widens competencies, then it also improves future welfare since the animal will be better able to withstand adversity, maintain health, reduce fear and achieve goals that will be sources of reward. However, in captivity, some of these potential welfare benefits may never be realized since the skills enhanced by play are never needed. Object play of captive felines thought to hone prey-capturing skills (Bateson et al. 1990) or rat play fighting thought to fine-tune body movement adjustments during sexual behaviour (Pellis & Pellis 2009) may serve as examples here. If the main fitness benefit of play indeed were greater proficiency in particular behavioural domains in adulthood, such as in sexual behaviour, prey capture or escaping predators, then changes in play frequency would have little welfare implication for captive animals. The reason is that these behavioural skills need not be brilliantly developed for captive animals to secure food, avoid predators and reproduce. However, if play contributed to more generic long-term skills, such as kinematic, behavioural and emotional flexibility, general stress resilience and communication and conflict-solving abilities, then implications for the welfare of captive animals would be more profound. While the basic physiological and survival needs of these animals are characteristically met by humans, captivity still presents a number of challenging and even stressful situations: the animals often live in barren environments, experience unpredictable and inescapable handling, or live at unnaturally high densities in groups of unnatural composition that may frequently change. At the same time natural features that facilitate social conflict resolution in the wild, such as space and hide-outs, can be absent. Findings on rat and primate social play, and also nonsocial play in other species, increasingly suggest that play may indeed equip animals with the general-purpose competencies and resilience outlined above (Donaldson et al. 2002; Von Frijtag et al. 2002; Fagen & Fagen 2004; Dudink et al. 2006; see also Pellis & Pellis 2009).

With immediate fitness benefits of play, the implications for welfare should be even more straightforward. A playing animal benefits immediately, not only potentially, from play and thus its welfare status should be enhanced. This is most obvious with its proposed function of manipulating the social environment. If, by playing with other individuals, the animal enhances its social status, decreases tension or attenuates aggression, it experiences less social stress (Palagi et al. 2006).

Does play always improve welfare? Not necessarily. In the cases of delayed fitness effects mentioned above, the potential future welfare benefits may remain unfulfilled. In other cases, the net welfare benefits for a group of animals may be nil. If skills that gain force through play are used in competitive situations then a gain in welfare by one animal may be offset by a mirror loss in welfare of the opponent. Playing, for example, may increase the competitive ability of an individual, which may result in a drop in social rank in others. In other situations, the positive effects of play may be accompanied by negative, but not symmetric, welfare effects in other group members. For instance, Soltis et al. (2003) found that adult squirrel monkeys, *Saimiri sciureus*, in captive groups could be strongly stressed by persistent play attempts of immature offspring that disrupt affiliations among the adults and increase their cortisol levels.

In summary, play is thought in the wild either to better equip animals for life in the future or to help them to minimize fitness risks in the present, at a cost. As such it potentially enhances future and current welfare in captive animals: while the costs of play are typically covered by humans, its proposed ultimate function of training general competencies in particular may improve biological functioning and welfare in captivity.

ANIMAL PLAY AS SPREADING GOOD WELFARE?

As noted already by Fagen (1981), Bekoff & Byers (1981), Gomendio (1988), Baerends (1989) and others, play is a contagious activity; just seeing animals playing can stimulate play in others (Bekoff 2001). Although empirical studies into this phenomenon are not numerous, they do confirm that play is contagious. The fact that exposure to more playful partners will stimulate play in others has been experimentally documented in laboratory rats (Pellis & McKenna 1992; Varlinskaya et al. 1999). Some correlational evidence also supports the notion that play is contagious. For instance, Leca et al. (2007) found that playful stone handling is synchronous in Japanese macaques and increases with group size, and they ascribed this phenomenon to the contagious nature of play. In addition, social play is sometimes reported as being polyadic (e.g. Petit et al. 2008; Palagi 2009) which can be ascribed to play contagion. The phenomenon of play contagion

seems to be widely recognized but its presence and magnitude in individual species still need to be examined.

As play behaviour (at least in mammals) seems to be accompanied by a specific emotional state, often labelled as pleasure or 'fun' (see above; also Špinka et al. 2001), the mutual stimulation of play can be viewed as a case of emotional contagion, a phenomenon that has been studied in humans for some time (Hatfield et al. 1994; Doherty 1997). Emotional contagion has only recently received research attention by ethologists, especially primatologists (Ross et al. 2008; Ferrari et al. 2009). New evidence suggests that cortical mirror neurons may provide a dedicated neural mechanism underlying emotional contagion: these neurons are activated both when an emotionally loaded behaviour is being perceived and when it is being performed (Ferrari et al. 2009). It has been suggested that this neural shortcut bypasses the need for complex cognitive appraisal of incoming stimuli and thereby enables the emotion to be copied very fast, sometimes in fractions of seconds (Ferrari et al. 2009). Indeed, the play stimuli to which other animals respond may be fully ritualized social play signals such as play faces in primates (e.g. Palagi 2006) or play bows in canids (e.g. Bekoff 1995; Rooney et al. 2001). In other cases, animals respond with their own play to elements of locomotor play by others; an example would be pirouettes and somersaults in bonobos (Palagi 2008).

Whatever its mechanisms are, the contagiousness of play is of relevance to animal welfare. If play activity of one animal can 'turn on' play mood and action in others then any play has the seed potential to generate more play with all its immediate and delayed beneficial consequences. Thus, raising play levels in captivity even by a moderate degree or only in some individuals may, through social amplification, result in substantial benefits in group-housed animals. How may this be achieved? Increased play in a group, for example, might initially be stimulated through small changes in housing conditions (e.g. Donaldson et al. 2002). Playback of play vocalizations could be investigated for its potential as a contagion, raising play levels in captive species for which such vocalizations have been identified (e.g. laboratory rats: Knutson et al. 1998; farmed mink, Mustela vison: G. Mason, unpublished data). Finally, domestic pigs and guinea pigs, Cavia porcellus, increase their locomotor-rotational play in response to a conditioned stimulus signalling the arrival of a reward (Dudink et al. 2006; B. Leci, N. J. Rooney & S. D. E. Held, unpublished data). This opens up the possibility of training one or several group members as 'play-seeds' to stimulate increased play in their group.

More research is clearly needed into the theory underlying the phenomenon of play contagion and its application to welfare assessment and improvement, bearing in mind that increased play in some group members may result in a welfare decrement in others (see previous section). Studies into this topic may benefit from using concepts and tools of the rapidly developing research area of behavioural, emotional and cognitive synchronization in animal and human groups (e.g. Raafat et al. 2009).

VARIABILITY OF PLAY: A STUMBLING BLOCK FOR USE IN ANIMAL WELFARE?

The potential contribution of the play–welfare relationship is now widely acknowledged in applied ethology and animal welfare science (e.g. Boissy et al. 2007; Oliveira et al. 2010). In the previous sections, we put forward evidence and arguments to examine its potential as an indicator of good welfare and also as an instrument for improving welfare; and we identified exceptions and knowledge gaps that caution against current adoption of play as a universal welfare indicator. Any efforts to realize the potential of play as a welfare indicator will encounter one further central difficulty: its immense flexibility and variability.

Play is variable across species. Almost all mammals play, and most of them socially. Among birds, only parrots, corvids, hornbills and Eurasian babblers have been recorded to play socially (Diamond & Bond 2003). Across mammals and birds, comparative studies have identified some general trends in ways in which play may vary systematically. For example, greater playfulness has been reported in species in which more growth occurs postnatally, that have larger total brain sizes, and in which specific brain structures, such as the amygdala and hypothalamus, are relatively enlarged (Pellis & Iwaniuk 2000; Iwaniuk et al. 2001; Diamond & Bond 2003; Lewis & Barton 2006). That said, even closely related species can vary considerably in their play behaviour as illustrated by the rat and the domestic mouse, Mus musculus: mice offer much locomotory play but little in the way of play fighting, which rats are famous for (Pellis & Pellis 2009). The reasons for much of this interspecies variability in play are unexplained (but see Pellis & Pellis 2009, for the rat–mouse comparison). Play research in any given animal may thus profitably start with a characterization of its species-specific play elements and their frequencies (e.g. Petrů et al. 2009). The same clearly applies to any play research in the animal welfare sciences where such characterization is needed before valid conclusions can be drawn about the welfare relevance of play in a given species. Because some species play much more than others, the importance of play as a welfare indicator and tool may differ between them.

Play also varies considerably within a given species. Whole wild populations or other groups of conspecifics can vary in the amount of play because of varied environmental conditions such as weather, food availability and habitat structure (Berger 1979; Barrett et al. 1992; Sommer & Mendoza-Granados 1995; Sharpe et al. 2002; Stone 2008). In captivity, similarly, herds, flocks or other animal groupings can differ greatly in play levels because of the specific conditions of their management such as nutrition supply, environmental complexity and perceived security (Bolhuis et al. 2005; Chaloupková et al. 2007). The correlation between play and welfare status may thus be particularly strong at the between-population level.

Furthermore, in many species, play differs between the sexes both qualitatively and quantitatively (Chau et al. 2008; Pellis & Pellis 2009). In domestic animals, differences have also been documented between breeds or strains (Walker & Byers 1991; Ferguson & Cada 2004). More importantly, how much an animal plays depends to a great degree on its age. Play typically has an inverted U-shaped distribution over ontogeny with highest frequencies occurring during infancy and the juvenile period (e.g. Byers & Walker 1995). A reduction in play during these periods may thus signal a welfare challenge and lead to current and future welfare decrements. During periods in an animal's life when play is naturally less frequent, its absence may be of little welfare consequence. This would be the case for adult or newborn animals in many species (but see Palagi & Paoli 2007; Cordoni 2009; Pellis & Pellis 2009 for examples of species with regular adult play). Where adult play is naturally rare, its occasional occurrence most likely indicates the animal is currently faring well. Spontaneously occurring, rare adult play in captive species thus holds particular promise, as well as methodological challenge for further study, as an indicator of good welfare. Documented case studies are rare by nature of their object. Anecdotal examples would be domestic sows and sheep leaping in simple, transient positive contrast situations such when moved from a barren to a strawed pen of equal size or when released from the shearer (see also Boissy et al. 2007). Whether adult animals also use play not only to self-medicate to relieve stress (Pellis & Pellis 2009) but also to stimulate their brains endogenously when external stimulation is low (as do bored human adults) suggests itself as an important question for further investigation.

Conspecific individuals of the same sex and age may still differ in their propensity to play or in their 'playfulness'. Biben & Champoux (1999), for example, reported a strong negative relationship between play levels and experimentally manipulated social stress levels in squirrel monkeys but also large individual variation in play levels within the same treatment groups. In dogs, where it has been most intensively studied, playfulness has been suggested as a stable personality trait (e.g. Svartberg & Forkman 2002) or as a behavioural characteristic related to several personality traits including 'sociability' and 'responsiveness to training', and also related to comparable traits in other species (reviewed in Gosling & John 1999; Jones & Gosling 2005). Finally, play frequency was also found to be moderately heritable in inbred Balb/c and DBA/2 laboratory mouse, *M. musculus*, strains (Walker & Byers 1991) suggesting a genetic component to individual differences in playfulness. Such interindividual variability has implications for using play behaviour as a welfare indicator as it means that individuals may differ in how quickly they give up playing under fitness challenge and how much they benefit from a given amount of play. Where welfare assessment is aimed at the individual animal, one would need to test whether being generally less playful might mean being generally in a less good welfare state. More often than not, however, welfare assessments aim to capture the welfare state of a group of animals, for example to examine the suitability of a given housing environment. If play behaviour is included in the assessment in such cases, it should be quantified for a representative number of group members to account for potential individual differences in playfulness.

In summary, variability in the amount of play shown by an individual or group can be partitioned by source into: variability caused by differences in welfare-relevant factors such as health, nutritive status, fear or environmental restriction of highly motivated behaviour; variability caused by other specific, but welfare-unrelated factors such as species, sex, age or personality; and random or 'error' variability not attributable to any specific factor. One challenge for a wider use of play in welfare assessment and improvement is to extract the first type of variability from the background of the latter two. While the principles outlined in the sections above potentially generalize across species, they thus need to be combined with an understanding of the sources of variability in play behaviour of each given species.

FINAL CONSIDERATIONS

Play: a Pain or Pleasure for Ethologists?

Behavioural science has, in spite of several decades of research effort, progressed much less in understanding play behaviour than, for instance, agonistic or feeding behaviour. Many students of play find the progress frustratingly slow. The classic hallmarks of play, that is, its appearance as a caricature of 'serious' behaviours, its intensely rewarding yet relaxed quality, its elusive function(s) and peculiar ontogenetic and phylogenetic distribution, have yet to be woven together into one consistent theory. That said, an integration of several theoretical strands seems to be drawing closer. In the following we attempt an outline of the loose network of current ideas about play among biologists. Play patterns may have their origins in situations in which young dependent animals enjoy a surplus of provisioning and relative safety (Burghardt 2005). Such situations provide unique opportunities for turning an awkward mix of juvenile and adult behavioural patterns into the 'what-if' games that young animals play with their own bodies, their physical environment and their companions. In this, young players forecast their developmental niche (Pellegrini et al. 2007) and boost the flexibility of their skills for the less forgiving challenges of adult life

to follow (Špinka et al. 2001; Pellis et al. 2010). The process gets its motivational and affective force by tapping into already existing reward mechanisms (Burgdorf & Panksepp 2006) thus generating a specific pleasurable, 'fun' aspect to play (Vanderschuren et al. 1997; Panksepp & Burgdorf 2010). This integrated play complex of developmental timing, behavioural organization, neuroaffective systems and evolutionary advantages of flexibility has evolved into different species-specific forms and thus produced the extant variety of play behaviour. The central idea of this proposal is that the key to understanding play behaviour is exactly the feature that was thought to be the main obstacle, namely its flexibility and inordinate variability. In short, the fluidity of play may be why play exists.

What we have outlined in the previous paragraph clearly still suffers from generalization and considerable speculation. Yet we include it in this review because, ultimately, the role of animal play in animal welfare will not be fully understood unless it is based on a clearer appreciation of the nature of play itself.

In Conclusion

Most animal play is easily blocked by detrimental environmental conditions, but under favourable conditions it can, through its rewarding, self-reinforcing properties, become prominent in the behavioural repertoire of infants and juveniles in particular. We have pointed to two self-reinforcing properties of play: first, play probably provides the animal with psychological benefits in the form of an opioid-mediated pleasurable experience, and animals that feel well will play more; second, play has a tendency to spread to other individuals, which may result in a contagious build-up of play in groups. These properties lead us to conclude that play should be investigated not only as a potential welfare indicator but also as an agent for improving the current and future welfare of an individual or a group.

Throughout this review we have sought to highlight welfare-relevant gaps in current knowledge of play behaviour, and to point to possible topics for further investigation. Finally, we suggest future research into the relationship between animal play and welfare may take two broad forms. First, it will define, describe and quantitatively analyse the species-specific play behaviour of the most important captive, domestic animals; and armed with this knowledge, it will investigate play as a welfare indicator and as a tool to improve welfare in the different species. Second, applied ethology and animal welfare science will work in tandem with other behavioural, neurophysiological, psychological, evolutionary and philosophical disciplines towards a deeper fundamental understanding of play as a unique behavioural phenomenon.

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