

Why do adult dogs ‘play’?

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ABSTRACT

Among the Carnivora, play behaviour is usually made up of motor patterns characteristic of predatory, agonistic and courtship behaviour. Domestic dogs are unusual in that play is routinely performed by adults, both socially, with conspecifics and with humans, and also asocially, with objects. This enhanced playfulness is commonly thought to be a side effect of paedomorphosis, the perpetuation of juvenile traits into adulthood, but here we suggest that the functions of the different types of play are sufficiently distinct that they are unlikely to have arisen through a single evolutionary mechanism. Solitary play with objects appears to be derived from predatory behaviour: preferred toys are those that can be dismembered, and a complex habituation-like feedback system inhibits play with objects that are resistant to alteration. Intraspecific social play is structurally different from interspecific play and may therefore be motivationally distinct and serve different goals; for example, dogs often compete over objects when playing with other dogs, but are usually more cooperative when the play partner is human. The majority of dogs do not seem to regard competitive games played with a human partner as “dominance” contests: rather, winning possession of objects during games appears to be simply rewarding. Play may be an important factor in sociality, since dogs are capable of extracting social information not only from games in which they participate, but also from games that they observe between third parties. We suggest that the domestic dog’s characteristic playfulness in social contexts is an adaptive trait, selected during domestication to facilitate both training for specific purposes, and the formation of emotionally-based bonds between dog and owner. Play frequency and form may therefore be an indicator of the quality of dog-owner relationships.

KEYWORDS:

domestic dog; play behaviour; dominance; predatory behaviour; neoteny

1. Introduction

Play behaviour continues to resist watertight definition, partly because it is almost certainly a heterogeneous category, and partly because unlike most other types of animal behaviour, its function and evolution are rarely obvious and have remained somewhat resistant to experimental resolution (Bekoff and Byers, 1998). Furthermore, in most species play is only common during the juvenile stage, so little comparative information is available for play by adults. It is traditional to divide play according to whether it is solitary (self-directed or at inanimate objects, i.e. object play) or social, but many animals use the same motor patterns in both, for example young domestic cats (West, 1974), suggesting that this may be a somewhat arbitrary distinction. Where more than one animal is involved, any definition needs to separate play from other, more “serious”, categories of behaviour from which many of the motor patterns used are self-evidently drawn, such as social conflict and sexual behaviour.

In terms of its form, play may be characterised as the performance of actions also performed in other contexts, but with variable (often reduced) intensity, and complex, apparently unpredictable sequencing, such that the goal with which the behavioural elements are normally associated, such as winning a fight or killing and consuming prey, is not reached (Bekoff, 2014). However, such stochasticity cannot on its own explain why two animals may engage in many bouts of wrestling without either ever injuring the other: individual animals do not escalate their aggression during interactions that they have somehow “agreed” will be playful. In some species the intention to play is signalled by discrete action-patterns used exclusively within the context of play, including the domestic dog’s play-bow and play-face (Bekoff, 1995). Individual bouts of social play are often prolonged by *role-reversal*, in which larger, stronger or generally more aggressive individuals momentarily perform behaviour more typical of smaller, weaker or more timid animals, in order to invite the resumption of a bout of play (Bekoff, 2014). Another suggested mechanism whereby this is achieved is *self-handicapping*, in which both participants make themselves vulnerable to (playful) attack (Spinka et al., 2001) although this is not ubiquitous, at least in domestic dogs (Bauer and Smuts, 2007). Such behaviour is superficially non-adaptive, since it involves an animal altering its trajectory away from the achievement of an immediate gain (winning) for the apparently more nebulous benefits of enhancing the probability that its partner will continue to play.

More generally, although play between juvenile animals may bring some immediate benefits, for example obtaining information about its physical and social environments (Held and Spinka, 2011), these are generally considered insufficient to account for its evolutionary persistence in the face of significant immediate costs (LaFreniere, 2011), which fall into three categories. First, play, while not metabolically expensive, may require a small increase in food intake (Martin, 1984), and consequently in many species declines in frequency when food is in short supply (e.g. Baldwin and Baldwin, 1976). One conspicuous exception to this general rule was found in young domestic cats, which increased the proportion of time that they devoted to object play when their mothers were malnourished (Bateson et al., 1990): this anomaly may be accounted for if object play in this species acts primarily as practice for hunting, in which such kittens will require proficiency earlier than their better-nourished counterparts, and this is supported by the motivational links between object play and hunting behaviour (Hall and Bradshaw, 1998). (To our knowledge, the effects of calorie restriction on play levels have not been tested in domestic dogs). Second, play may also

expose juvenile animals, even well-fed ones, to the attention of predators (e.g. Harcourt, 1991), and as predicted, predator odours do inhibit play (Siviy et al., 2006). Third, both play-fighting and exploratory play must also carry some risk of injury (for further discussion on the costs of play, see Graham and Burghardt, 2010).

Taken together, such costs should, unless at least balanced by benefits, act as an evolutionary brake on play behaviour. However, in many species, motivation for play in young animals appears to be remarkably strong, for example producing a strong rebound effect if prevented for a period of time (LaFreniere, 2011). Thus functional explanations for play behaviour have come to rely upon the use of life-history theory, invoking delayed benefits of play that have a robust effect on lifetime reproductive success, including the development of skills for finding food, and for competing with conspecifics.

Play is generally much less frequent in adult animals than in juveniles, and has received much less research attention (Hall, 1998). Even closely related species may differ considerably in the extent to which play persists into adulthood. For example, in common chimpanzees *Pan troglodytes* object play declines rapidly with age, whereas in bonobos *Pan paniscus* juveniles play with objects almost as often as infants do, and even adults play regularly (Palagi and Cordoni, 2012). This difference suggests further functions for play, since bonobos also show distinctly higher rates of sexual behaviour than common chimpanzees. Play has been posed to function in the attraction of possible mates (Held and Spinka, 2011), and it is feasible that play functions as a “peacock’s tail” in other species, in which animals with excess resources can signal their reproductive potential through the intensity of their play. In the case of dogs the role of play in intra-specific mate selection is unstudied, but it is possible that playful dogs are preferred during artificial mate selection by humans.

1.1. Play in domestic Carnivora

Both the domestic cat *Felis silvestris catus* and the domestic dog *Canis lupus familiaris* play much more frequently than their wild ancestors, possibly an effect of behavioural neoteny imposed by domestication (Driscoll et al., 2009). These two species have therefore provided convenient models for the study of play in the Carnivora as a whole (e.g. Bekoff, 1995; Hall, 1998). Whatever the underlying mechanism, in their modern context as companion animals, play in these two species appears to have very different motivations. Play performed by adult domestic cats is most commonly directed towards prey-like objects, and is structurally and motivationally very similar to hunting behaviour (Hall, 1998; Hall et al., 2002). In the domestic dog, play is more likely to involve a partner, whether canine or human, and appears to have a predominantly social motivation (Pullen, 2011; Rooney et al., 2000; Ward and Smuts, 2007).

It is not straightforward to elucidate for either species what the function of play (in the evolutionary sense) by adults might be, since reproductive success in both is nowadays strongly influenced by anthropogenic factors. Cats are generally asocial animals, and play does not appear to feature in courtship behaviour (Liberg et al., 2000). Dogs, by contrast, are highly social, and it has been suggested that social play may have a role in influencing the outcome of more competitive relationships (Bauer and Smuts, 2007; Trisko, 2011). The costs associated with playing in wild animals (energy consumption, exposure to predators, risk of injury) are considerably less in companion animals than in wild animals, lifting the evolutionary pressures that would otherwise lead to a reduction in motivation to play in life-

stages where it has little benefit. Readiness to play in domestic dogs may therefore simply be no more than a side-effect of breeding for other desirable traits, such as the truncation of the hunting sequence to produce herding, retrieving and guarding breeds (Coppinger et al., 1987), or linked to desirable physical features such as those contributing to “cuteness” (Sherman and Haidt, 2011). However, research into play in dogs has focused almost exclusively on companion dogs, and it has recently been estimated that worldwide these may be outnumbered by free-ranging dogs by three to one, even today (Lord et al., 2013): the selection pressures that shaped the extension of play into adulthood in the domestic dog may therefore not have been entirely or even primarily anthropogenic. Nevertheless, it is possible that over the course of domestication play has become an important component of social interaction between dog and man, and has thereby been selected for, with a general tendency towards playfulness then affecting intra- as well as inter-specific social play.

Bekoff (2014) and others have proposed that play not only allows the practice and development of social skills, but also, more controversially, may teach animals the difference between ‘right’ and ‘wrong’, helping “in the development of fairness and moral sentiments, as well as social justice” (Bekoff, 2014 pp 63-64). For example, Bekoff and Pierce (2009) consider that dogs practice what they call ‘fair’ play, whose four ‘rules’ are “Ask first, be honest, follow the rules, and admit when you’re wrong”. While there is increasing evidence that play does bring such benefits to our own species, and possibly to higher primates (LaFreniere, 2011), it seems less likely that the cognitive abilities of dogs and other members of the Carnivora extend to such abstract concepts (Horowitz, 2012). The attribution of abstract concepts such as “social justice” to dogs may be a reflection of the ease with which dogs are (often unintentionally) over-anthropomorphised (Bradshaw and Casey, 2007; Kwan et al., 2008). A simpler explanation, which parsimony suggests should be considered whenever possible, is that experience of playing allows a dog to learn which actions best encourage the perpetuation of play. thereby maximising for each individual the benefits, both immediate and long-term, that play must (presumably) afford.

In the domestic dog, the term “play” has thus been used to cover a variety of types of behaviour: solitary play directed at objects, intraspecific and interspecific social interactions, some of which include objects but many of which do not. It is unlikely that such a wide variety of interactions could be ascribed to a unitary motivation or function, and we will therefore consider each in turn.

2. Solitary object play

Most companion dogs seem to prefer to use objects in the context of interactions with people rather than play with them asocially (Pullen, 2011). However, they do manipulate objects in non-social contexts, and the wide range of ‘dog toys’ designed for solitary play testifies to the belief that this is beneficial to their dogs’ well-being, even though such effects appear to be small, at least in kennelled dogs (Wells, 2004). The motivation for solitary object play may be quite distinct to that when the context is primarily social, so we will consider the former first. As with domestic cats, the types of toys that dogs prefer - friable, noisy toys that move unpredictably - seem to mimic the properties of their ancestor’s typical prey (Pullen et al., 2010). Confirming the general impression that dogs easily become ‘bored’ with toys, and that they are strongly neophilic towards new objects (Kaulfuß and Mills, 2008), objects that initially induce play become rapidly habituated to (Pullen et al., 2012). However, motivation

to play can remain high even after play with a specific toy has ceased: disinhibition can be both instant and complete even when the object changes very little. For example, when a toy that has been played with to the point of habituation is exchanged for an otherwise identical toy, play may resume at its original intensity: presumably the difference perceived by the dog is that the new toy is not contaminated with its own saliva (Pullen et al., 2012). Thus solitary object play in dogs appears to be both structurally and motivationally related to predatory behaviour.

A quite different motivation is likely to be involved when the “toy” contains edible components. Kennelled dogs spend longer interacting with friable “toys” such as bones than they do with other rubber toys (Hiby, 2005), and daily delivery of food-filled “toys” leads to anticipatory behaviours in many dogs, and a reduction in self-mutilation and stress-related behaviours in some (Gaines, 2008; Hiby, 2005). Cessation of daily food enrichment leads to increased urinary cortisol levels in some dogs, whilst re-enrichment is accompanied by reduced physiological stress levels. The dogs showing such reactions are significantly more likely to be those that utilised the devices the most, showing that these devices are highly valued by some but not all individuals (Gaines, 2008). However, it is unclear whether interaction with a food filled device is play, or simply driven by a motivation for oral manipulation. The finding that daily provision of a food filled “toy” is not accompanied by a reduction in the dog’s motivation to undertake a task rewarded by human led object-oriented play (Gaines et al., 2008) suggests that these two interaction types are separately motivated.

3. Social play involving objects

Objects take on a quite different significance when they are involved in social contexts, both intra- and inter-specific, since an object held by a person is more interesting to a dog than the same object held by a mechanical device (Rooney, 1999). It is also possible that some apparently solitary play has the goal of attracting a social partner, although this appears not to have been tested formally. A majority of dog owners use objects as the focus for playful interactions with their dogs: in one survey conducted in the UK, the commonest of these was “fetch” (retrieval of an object thrown by the owner), and “tug-of-war”, in which the two participants simultaneously pull on the same object, with the apparent intention of gaining sole possession (Rooney and Bradshaw, 2003). In the past it was widely promulgated that the winning or losing of such games could have profound effects on the quality of the owner-dog relationship, and specifically that allowing dogs to win repeatedly could encourage them to become aggressive or “dominant” (e.g. O’Farrell, 1992; Rogerson, 1992). However, our observations and testing of dog-owner relationships found no evidence for this: those dogs whose owners allowed them to “win” tug-of-war games showed no consistent differences in behaviour from those that were not allowed to win (Rooney and Bradshaw, 2003), and similarly Tóth et al. (2008) found no connection between the playing of object-orientated games and competitive behaviour in non-playful contexts. When we experimentally manipulated the proportion of wins to losses in a group of golden retrievers, no change in confident behaviour (= that commonly described as “dominant”, such as standing over the (supine) owner, high stance and tail position) could be detected, but there was an increase in “obedient attentiveness” (a factor combining behaviours such as pricked ears, offering a paw or licking the experimenter, and shorter latency to comply with commands) towards the person who played with the dog between the first and last of the twenty games (Rooney and

Bradshaw, 2002). These dogs were more spontaneously playful after winning ten consecutive games than after losing ten games, suggesting that winning may simply be more rewarding than losing.

When studying dog-owner dyads (Rooney and Bradshaw, 2003), we found that those owners who reported that their dog regularly initiated play were also significantly more likely to report aggression (defined as “any exhibition of growling (not playful), baring teeth, snapping or biting” toward them) and to perceive the dog to be “dominant” (possibly because many owners seem to equate aggression with “dominance”). When tested, these dogs were found to be less “amenable” (a factor linking behaviour patterns traditionally described as submissive, such as low posture). This suggests that owners who allow their dogs to initiate play may also be more likely to allow them to determine the timing of other interaction and hence such play may be symptomatic of a type of ownership style. It also highlights the importance of human-dog play signals (Rooney et al., 2001), which usually communicate the playful context to the dog, but which may be lacking in such play-initiating dogs.

Dogs playing together also compete over objects, sometimes playfully and sometimes more agonistically. We compared dog-dog and dog-human object-oriented play using the same subjects (Labrador retrievers) and the same toys (lengths of knotted rope), and with the humans imitating dogs as closely as possible, e.g. not throwing the toy, or raising it above the dog’s head. We found that dog-human play was more collaborative overall (Rooney et al., 2000). When only one toy was made available, dogs frequently surrendered the toy to the person, prolonging the play, but once they had gained possession, rarely surrendered the toy to the other dog. When two toys were provided, the two dogs tended to each play with one each, but when the play partner was human, whichever toy was not being held was often ignored. Hence we suggest that for most dogs the motivation for inter-specific object-oriented play is primarily to interact with a person, rather than trying to gain possession of the toy(s).

4. Social play - without objects

Play involving two (or more) dogs often takes the form of play-fighting, sometimes referred to as ‘rough-and-tumble’ play, interspersed with bouts of chasing that lead to further physical contact (Burghardt, 2005). Play-signals, including the play-bow, are often used both at initiation and throughout play to indicate the non-serious nature of the interaction that follows (Bekoff, 1995; Horowitz, 2009). Interspecific play, i.e. between a dog and a person, is also preceded by and interspersed with play-signals, although the effectiveness of those emitted by the human participant is highly variable (Rooney et al., 2001) and many may simply act to direct the attention of the dog (*sensu* Horowitz, 2009). Owners report employing a wide variety of actions to initiate play (Rooney et al., 2001). Some of these show obvious structural similarities to intraspecific canid play signals, such as play-bows and exaggerated approach/withdrawal (Bekoff, 1995). Other reported signals, including whispered vocalisations, clapping, and blowing at, shoving, tapping or grabbing the dog are specific to the dog-human context, and their effectiveness varies markedly between partnerships, likely as dogs learn the significance of their individual owners’ habitual actions (Rooney et al., 2001).

While play-fighting can occur between dogs that are unfamiliar with one another, play is sustained for longer when the dogs have played together before (Pullen et al., 2013). In relationships that are already well-established, the two dogs play according to sets of “rules”

that are specific to that dyad: the same dog may exhibit self-handicapping when playing with one dog, while always attempting to win with another (Ward and Smuts, 2007; Ward et al., 2008). Thus learning appears to play a major part in determining the form which play-fighting takes between any pair of dogs, and with repetition may come to be a non-harmful mechanism for reinforcing established relationships (Trisko, 2011). When the play is consistently one-sided, i.e. the stronger participant never self-handicaps, the motivation of the ‘underdog’ to continue to initiate play may seem unclear (and in dog-human play, motivation to play declines if the human partner always wins, see section 4). Such heavily asymmetric play may be a way in which the weaker dog can test the other’s strength without making a potentially injurious direct challenge, but anecdotally it appears that such relationships can remain one-sided even when the originally stronger dog has aged to the point where it would seem incapable of fighting effectively should the originally weaker dog choose to mount a serious challenge. Thus play-fighting may be more important in maintaining social cohesion as such, rather than the primary objective being to assert and then maintain “dominance” (Bradshaw et al., 2009).

‘Rough-and-tumble’ play is also widely practiced by owner-dog pairs, and more so by male than female owners (possibly related to the reluctance of males to engage in other types of close physical contact: Rooney, 1999). Owners use a wide variety of signals, some more effective than others, to indicate the playful context of the interaction (Rooney et al., 2001). Whether or not these games have a significant effect on the relationship between dog and owner is hotly debated (Rooney and Bradshaw, 2003) but remains unclear. We found that the dogs of owners who choose to wrestle with their dogs showed a different quality of attachment to those that chose not to (higher amenability and lower separation-related behaviour) but these differences could simply reflect the dog’s or the owner’s preferences, rather than the way that the owner plays with the dog directly affecting their relationship (Rooney and Bradshaw, 2003).

5. “Eavesdropping” during dog-human play

Since it seems likely that dogs extract socially-useful information from playing with other dogs, it is also possible that they might do so by observing games that they are not participating in. Social learning by dogs has attracted a great deal of research attention recently (Pongrácz, 2014), and play would seem *prima facie* to be a good context in which this could occur. In social groups of three or more, dogs appear to be able to extract reputation-like inferences from the observation of play bouts in which they are not themselves involved (Rooney and Bradshaw, 2006). Play is not unique in this respect: playful interactions appear to be just one of several different contexts in which dogs can observe and assess other dogs’ behavioural traits and strategies (e.g. Kundery et al., 2011; Marshall-Peschini et al., 2011), although precisely what information dogs extract from observing such third-party interactions is still unclear (Freidin et al., 2013).

Counter to predictions based on “dominance theory” spectators show no evidence of deference or submission to winner, but rather are keener to approach both dogs and humans when they have just “won” a playful encounter. When vision is blocked dogs still distinguish between human- and dog-won games, hence information must be available from vocalisations and post-play signals from the dog, as well as visual cues (Horowitz, 2009; Rooney and Bradshaw, 2006).

6. Play as reward

Dogs are powerfully rewarded by social contact with familiar humans (Fonberg et al., 1981; although see Feuerbacher and Wynne 2014), as attested to by the use of play between dog and handler as the main reward in the training of working dogs (e.g. Svartberg, 2006), including detection (“sniffer”) dogs (Rooney et al., 2004), guide dogs for blind people (Naderi et al., 2001) and search and rescue dogs (Mariti et al., 2013). Recent observations of dog-owner dyads show that those owners who were most involved when playing with their dog, also had dogs which scored generally higher for obedience to basic commands, supporting the potential value of play as a reward for training (Rooney and Cowan, 2011).

Affiliative play is associated with a reduction in the stress hormone cortisol, consistent with such play being rewarding, whereas cortisol rises following play that includes verbal correction (Horváth et al., 2008), suggesting that any reward value in such play is more than cancelled out by the aversive nature of the handler’s vocalisations. Positive interactions between dogs and humans, including play, result in neurophysiological changes in both human and canine participants, including increased beta-endorphin, oxytocin, prolactin, beta-phenylethylamine, and dopamine (Odendaal and Meintjes, 2003). These, accompanied by pleasurable feelings, may strengthen the bond between dog and human. Such dog-induced positive affect may conceivably have contributed to humans selecting playful dogs during domestication and thereafter.

7. Play as a contributor to, and sign of, well-being

Intraspecific play behaviour has been posited as an indicator of positive affective state (e.g. Held and Spinka, 2011), since play is usually only seen when conditions are optimum (e.g. Jensen et al., 1998) and animals are relaxed (Berman, 1980). It may also be indicative of a positive well-functioning relationship (Rooney and Bradshaw, 2003). Among pet dogs, frequent and/or more intense play dog-human play is associated with higher levels of obedience (Arhant et al., 2010; Rooney and Bradshaw, 2003). This may arise in those relationships where play has been used as a reward in training, but it also suggests that play may reinforce the bond between dog and owner. The quality of the play exchanged may also be important. During observations of dog-owner partnerships Rooney and Cowan (2011) found that dogs reported to have been trained for more tasks using physical punishment based methods were generally less interactive during play with their owner, whilst Rehn et al. (2014) observed less independent play in dogs which interacted more frequently with their owner. Hence both quantity and quality of play may be indicative of positive affect within a dog owner relationship.

8. Conclusions

At least as applied to domestic dogs, behaviour that is loosely categorised as “play” is, on closer inspection, highly heterogeneous. The description of such behaviour as “playful” therefore appears to be predominantly anthropomorphic, grouping together superficially functionless activities that are presumed to be “fun”, i.e. associated with positive affect. The

various types of play that we have distinguished are distinctly motivated and occur under different circumstances, and are therefore likely to have been affected by different evolutionary pressures.

Solitary object play in the domestic dog appears similar, both in its morphology and its motivation, to predatory behaviour, as also found in the domestic cat. Unlike the cat, which retains fully functional predatory behaviour (Bradshaw et al., 2012), dogs of different breeds selectively perform specific elements of their ancestral predatory behaviour, while others are inhibited (Coppinger et al., 1987). This suggests that solitary object play by adult dogs may not be adaptive in its own right, but rather a by-product of the deliberate selection for disruption of the sequencing of predatory behaviour that has produced the non-hunting breeds of dog (Coppinger et al., 1987). One prediction of this hypothesis is that there should be breed differences in both the form and intensity of solitary object play, related to the function for which the breed was derived, but no systematic study of this appears to have been done.

Turning to social play, both with and without objects, we have postulated that play between a dog and a person and two dogs are motivationally and functionally distinct. However, it is also possible that since dogs may have little concept that the other participant has intentions (Bräuer, 2014), social play might conceivably be a homogeneous phenomenon, with the variations that we have described depending mainly on the morphologies of the participants (e.g. dogs can't throw sticks) and the relationships between them. Thus depending upon which of these is correct, selection for playfulness in adult dogs may either have acted upon intra- and inter-specific play separately (assuming they are distinct phenomena), or primarily on only one, with the other being a side-effect or spandrel.

Intraspecific social play is commonplace, though not universal, among pet dogs. Most individuals will attempt to initiate play with other dogs, and playful interaction, while far from universal, is more common than agonistic interaction (e.g. Trisko, 2011). Play between adults has received little attention in studies of free-ranging and feral dogs, but it is likely that when there is competition for key resources such as food and access to mates, dogs become less playful and more agonistic: this has been demonstrated experimentally in the arctic fox (Frafjord, 1993). Free-ranging dogs currently outnumber companion and working dogs, and may conceivably have done so throughout domestication. Thus it is possible that the selection pressures that have favoured dogs that continue to play into adulthood have acted primarily on intraspecific play. To date, the few studies of play behaviour in free-ranging dogs have concentrated on juveniles (e.g. Pal, 2010), and the traditional dominance-submission framework has been used to summarise interactions between adults (Bonanni and Cafazzo, 2014): it would be interesting to examine whether alternative conceptions of free-ranging dog society could be derived from such playful interactions, or whether these are simply too rare to be important.

More plausibly, in our view, the playfulness of adult dogs could have been selected for during domestication, as an adaptive trait facilitating differential resource provisioning by humans. Dogs may be unique among the animal kingdom in the extent to which they are rewarded by affiliative social contact with humans - and within that context, by play. Repeated play appears to be a major factor in enhancing the relationship between dog and owner, and given that this link seems to be absent in wolves, may have been selected for during domestication. It may have evolved through natural selection during the early stages of domestication:

playfulness being one of the triggers for the “cute” response in humans (Sherman and Haidt, 2011; Waller et al., 2013), those wolves most inclined to engage in playful interactions with humans may have been more highly valued, and hence given more resources, than less playful individuals were. Then, as attempts were made to train proto-dogs for specific tasks such as hunting and guarding, learning might have been fastest in those individuals which found social interaction, and especially play, rewarding. More generally, dogs that would play with people may have been preferred not only because playful interaction is enjoyable for the human participant but also because it allows opportunities for social interaction outside the more conventional framework of control, that of dog and master (Rooney, 1999). Latterly, playfulness may have been selected for deliberately, both to generate neotenic breeds that would appeal directly to potential owners, and possibly also as part of a suite of behaviours emphasising juvenile characteristics and trainability as an alternative to the generally less desirable traits of high aggressiveness and competitiveness. Thus overall domestic dogs’ playfulness may have made them more useful to mankind, as well as simply more intrinsically appealing.

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